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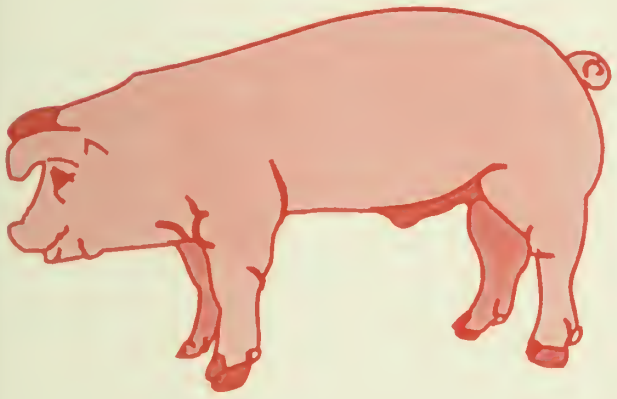

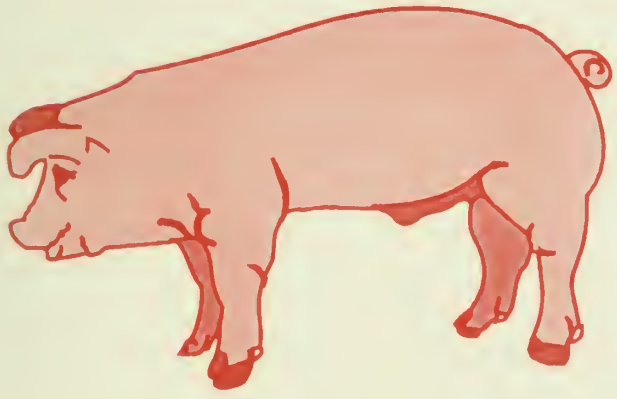

University of Illinois

PORK INDUSTRY CONFERENCE

"Swine Energetics"

December 4-5, 1996

College of Agricultural, Consumer and Environmental Sciences
Department of Animal Sciences
Cooperative Extension Service
Agricultural Experiment Station
University of Illinois at Urbana-Champaign

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PORK INDUSTRY CONFERNCE
December 4-5, 1996
Jumer Castle Lodge, Urbana, Illinois

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Swine Energetics - What Does this Mean?

Dr. Robert A. Easter, Professor and Head

Department of Animal Sciences, University of Illinois, Urbana-Champaign

Welcome to the University of Illinois Pork Industry Conference. We believe this to be the premier educational event organized annually by the swine faculty in the Department of Animal Sciences. Your attendance and interest in our program are appreciated.

The Pork Industry Conference was developed in the late 1970's as a replacement for the traditional University of Illinois Swine Day that had been held on the campus for many years. This was a time of great profound change in the swine industry. Specialized confinement production systems were being constructed throughout the Midwest and the Animal Science faculty lead, by Professor Dick Carlisle and Department Head, D.E. Becker, recognized the need to provide a forum for the discussion of innovative technology. Dr. Gilbert Hollis organized the first Illinois Pork Industry Conference in 1977 and has lead each conference since then. Thanks, Gilbert, for a job well-done.

The organizers of each Pork Industry Conference have focused on one or more rapidly developing areas in swine technology. The central theme this year is swine energetics. It is arguable that no area, other than water, has received less attention than the pig's energy needs for growth, maintenance and successful reproduction. Undoubtedly, this is in part a consequence of the abundance and consistent supply of calories found in the ubiquitous midwestern corn-soybean meal diet.

Energy nutrition affects many factors that influence pig performance. The pig's capability to achieve it's potential for lean growth is dependent on an adequate energy intake. Differences in growth rate among genetically similar pigs can be attributed in large part to variations in feed, and thus, energy intake. Excess energy consumption inevitably results in fattening, often beyond a point that is desirable. Management practices, equipment design, climatic environment and genotype are only a few of the many factors that affect energy intake and efficiency of converting dietary energy to lean, marketable pork.

You will find that many of these topics are addressed in the papers included in these proceedings. One topic is not. Earlier this fall, the Food and Agriculture Organization of the United Nations convened a World Food Summit in Rome, the first of its type in almost a decade. This conference reflected a growing concern that global population growth is, again, exceeding the rate of increase in food production. The food energy needs of humanity are described in the conference technical papers that are now available via the world wide web. Doubling the world's output of food energy in the next 40 years will be necessary. Without major technical breakthroughs, the era of abundant and inexpensive energy for swine feeding may be nearing an end. Efficiency of feed energy use by pigs will be essential to future success.

As you visit with members of the Animal Sciences faculty, you may hear reference to the Illinois Swine Initiative. We have recognized for several years that the educational needs of the swine workforce are changing. Production systems have increased greatly in sophistication and technological change is occurring at an ever-increasing rate. At the same time the population of students with experience in the real-world of swine production is very small. Last year our department embarked on a major program to overhaul the way in which we prepare undergraduate and master's students for employment in the swine industry. Courses have been revised, new requirements for field experience are being introduced and the first students have been accepted into a master's of "pigology" program.

The technology transfer program is being revised as well. Following leadership initially provided by faculty in Agriculture and Consumer Economics, PorkLift is being expanded as a world wide web-based method of information transfer freely available to the producers of Illinois. The first swine production class taught with distance education technologies is being offered by campus-based faculty this fall at sites in Rockford and East Peoria. In the next few years we expect greatly to expand our capability to deliver full-length courses, short-courses and seminars to locations around the state, nationally and internationally.

Thanks for coming to the Pork Industry Conference. We believe your time will be well invested.

Fat as an Alternative Energy Source

Tim S. Stahly, Ph.D.
Professor, Iowa State University

The lipids in feedstuffs commonly consumed by swine consist mainly of neutral fats, specifically triglycerides. The concentration of fats in feedstuffs varies widely. Fat levels range from 1.5 to 4.5% among cereal grains, 4.5 to 10% among high oil corn lines, .5 to 9% in fibrous byproducts, .5 to 20% in common protein feedstuffs, and 90 to 99% in supplemental fat sources. Consequently, the level of fat in a particular diet is dependent on the type of basic feedstuffs included as well as the level of a supplemental fat source. For example, corn (standard yellow dent) and wheat contain about 3.9 and 1.7% fat, respectively. Inclusion of wheat for corn in a simple corn-soybean meal mix effectively lowers the fat content of the diet by one-half. Similarly, the replacement of half of the dehulled soybean meal (.8% fat) with full-fat beans (18% fat) as the supplemental protein source in a corn-soy mix raises the dietary fat content from 3 to above 5%. Supplemental fat sources commonly used in swine diets include animal fats (tallows, greases), vegetable oils (corn, soybeans), restaurant greases (spent oils and greases), and commercial blends (mixtures of vegetable oil, animal fats, restaurant grease).

The composition of these fats largely differ in the type of fatty acids, the building blocks of fat, that are present. Animal fats normally contain more saturated fatty acids which are a solid at room temperature. Vegetable oils largely consist of unsaturated fatty acids which are liquids at room temperature. The composition and physical form of restaurant grease and commercial fat blends depend on the ingredients present in the mixtures although vegetable oils normally predominate.

The primary contribution of fat for swine is that it serves as a concentrated source of energy-yielding ingredients. The response of pigs to dietary fat additions largely depends on the animal's feed intake level, the digestibility of the fat source, and the efficiency of utilization of the fat for body maintenance and tissue growth (i.e., muscle and fat).

Pigs of all ages have a preference for diets containing fat. In preference tests, pigs will favor the consumption of the fat supplemented diet 60 to 80% of the time. When given ad libitum access to a single diet only, fat additions normally result in a 1 to 3% higher level of energy intake, particularly in pigs housed in a warm environment. In a cold environment, the feed intake response to fat is less consistent and smaller in magnitude.

Most fats are well digested by the pig except possibly for the first one to two weeks after weaning. The digestibility of a specific feed fat largely depends on the ratio of unsaturated to saturated fatty acids in the total diet (Figure 1). If the unsaturated to saturated ratio of fatty acids exceeds 1.5 to 1, digestibility of fat is high. The unsaturated to saturated ratio in common feedstuffs range from

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Presented at the University of Illinois Pork Industry Conference on December 3-4, 1996, in Urbana, Illinois.

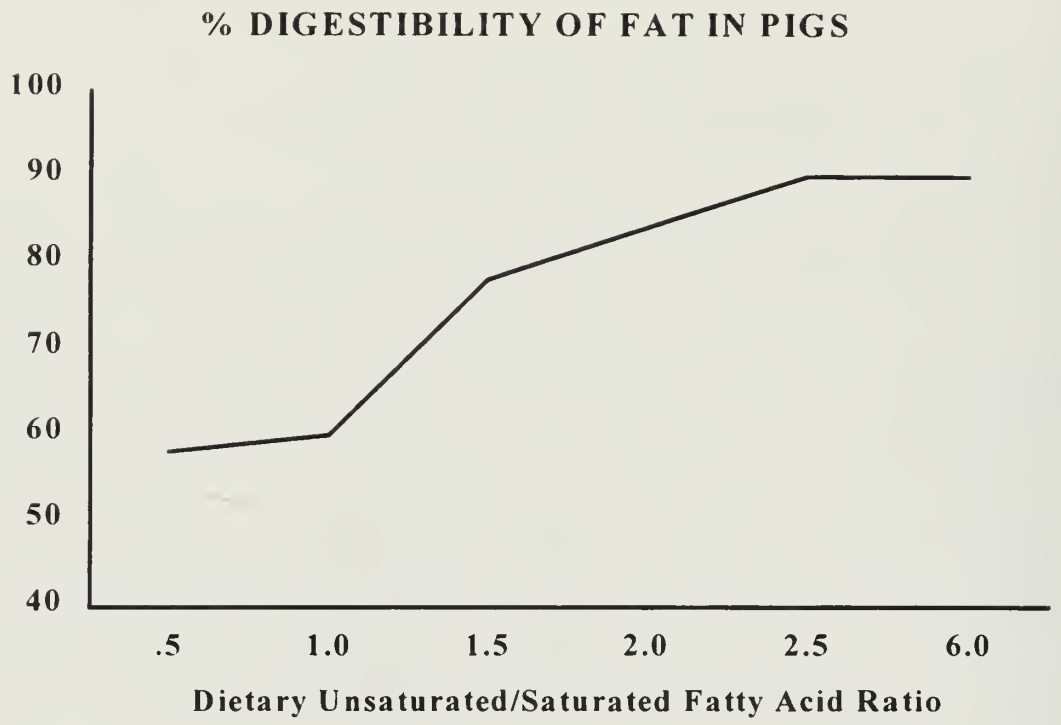

Figure 1. Digestibility of dietary fat in pigs as influenced by the ratio of unsaturated to saturated fatty acids in the total dietary fat mixture (Stahly et al., 1984).

.8 (beef tallow) to 6.0 (vegetable oils). Corn-based diets normally exceed the 1.5 to 1 ratio regardless of the supplemental fat source because the 4% corn oil in corn is so unsaturated. However, in diets based on low-fat feedstuffs, such as wheat (1.7% fat) or dried skim milk (.8% fat), the fatty acid composition of the saturated fat source may become important. The digestibility of fat, particularly saturated fats, also is reduced to a limited extent (1 to 6 percentage units) by inclusion of fibrous feedstuffs and high levels of calcium and magnesium in the diet.

The efficiency of use of dietary fat in the pig depends on what it is utilized for in the animal's body. Fat absorbed from the digestive tract can be deposited directly into body fat tissues. This process is very efficient and results in a minimum los of energy as body heat. In contrast, fat as well as starch (i.e., cereal grains) must undergo metabolic transformations to be utilized for body maintenance functions or growth of muscle tissue. These transformations are associated with a significant loss of energy as body heat. Thus, the energy content of fat is used most efficiently or has its greatest value in pigs when it is deposited as body fat. Conditions that maximize feed (energy) intake and minimize nutrient needs for body maintenance (i.e., warm environment) will allow the greatest opportunity for efficient body fat deposition and thus dietary fat utilization. Restricted levels of feed intake or production conditions that require more feed for body maintenance (i.e., cold environment) will increase the portion of fat that must undergo metabolic transformation and the associated inefficiencies of use.

The energy value of a pound of digestible fat source in pigs allowed to consume feed ad libitum is estimated to be 3.8 times that of a pound of corn for pigs housed in a warm environment versus only 2 times the value of corn in a cold environment. If feed intake is restricted due to overcrowding, limit feeding practices, postweaning food intake slump, the relative energy value of fat may be lowered.

The economic value of dietary fat can be estimated from the impact of dietary fat additions on the days required for pigs to reach market weight, the pounds of feed required per pig, and the pig's carcass merit (i.e., backfat thickness or lean content). The growth response of growing pigs (from 50 to 250 lb body weight) to each net addition of 1% dietary fat is shown in Table 1. The magnitude of the response to added dietary fat is linear for diets containing 3 to 12% total fat. Furthermore, the growth response to dietary fat does not differ substantially among pig genotypes or genders differing in their capacity for tissue growth, although these relationships have not been studied extensively.

Table 1. Response of pigs (fed from 50 to 250 pounds) to each 1% net addition of dietary fat.[a]

Production of	Thermal Environment[b]	
Market Pig	Cold	Warm
Days to market	-.25	-1.6
Feed/pig, lb	-7	-13
Carcass backfat, in	+.011	+.024

[a]Responses estimated from data summarized by Stahly (1984). Pigs self-fed grain-soybean meal diets adequately fortified with amino acids. Supplemental fat source assumed to be 88% digestible.
[b]Cold and warm environments represent climate conditions equivalent to 5 to 15°F below and 0 to 15°F above the pigs' lower critical temperature at each stage of the pigs' growth.

To calculate the economic value of fat, the non-feed fixed costs (dollar/pig/day for building and equipment charge, labor cost, etc.), feed cost (dollar/pound of feed), and premiums-penalties for carcass leanness (dollar/1 inch backfat/pig) must be estimated for each production-market situation. Based on assumed fixed and feed costs of $.14/day/pig and $.07/pound with market incentives of $10.00/1 inch/pig, the break-even value for the dietary inclusion of x% added fat (e.g., 3%) can be approximated.

Pig response = 3(-1.6 days) + 3(-13 lb feed) + 3(+.024 inches backfat)
= -4.8 days - 39 lb feed + .072 inches backfat

Change in production cost - market value:
= -4.8 days ($.14/day) - 39 lb ($.07/lb) + .072 inches (10.00/inch)
= -.67 - 2.73 + .72
= -$2.68/market pig

Based on the assumption that pigs were fed a basal diet from 50 to 250 pounds body weight and required 580 pounds of feed/market pig, the quantity of the 3% fat added diet (580 - 39 = 541 pounds) needed to produce a market pig is worth up to $2.68 more than the non-fat basal diet. If the basal diet is valued at $.07/pound or $140/ton, the fat-added diet is worth $.07/pound + $2.86/541 pounds of feed = $.07 + .0053 = $.0753/pound or $150.6/ton. If the fat supplemented diet can be produced (including additional fat transportation, storage, mixing costs) or purchased for less than $150, it would be economically desirable to do so. This cost also must include the expense of any additional nutrient-compound fortification (i.e., protein, antioxidant) needed in the fat-supplemented diet. Obviously the added value of the fat-supplemented diet is reduced for pigs housed in a cold environment and in operations with lower non-feed fixed costs and feed costs or those receiving a greater penalty for fat carcasses.

Future economic consideration relative to dietary fat additions also will include the influences of dietary fat on pork quality, the immune status of pigs, and possibly animal waste production. Dietary fat additions result in both positive and negative effects on pork quality. As dietary fat concentrations increase, the intramuscular fat content of pork products also increases (Table 2). This result is associated with greater consumer sensory satisfaction based on taste tests.

Table 2. Impact of dietary fat on fresh pork quality.[a]

Muscle Trait	Lean Genotype	Dietary Energy Source		Unit Change
		Starch	Fat	
Water loss, % (during 9 days of retail storage)				
	High	13.6	10	-3.6
	Mod	13	11.1	-1.9
	Low	7.4	7.4	0
Color (paleness of pork after 9 days of retail storage)[b]				
	High	49.1	47.2	-1.8
	Mod	45.9	44.8	-1.1
	Low	44.4	44.1	-0.3
Intramuscular fat, %				
	High	2.35	3.27	+.9
	Mod	NA[c]	NA[c]	
	Low	6.78	7.61	+.8

[a]Stahly et al. (1997). The diets consisted of a basal corn-soybean meal mix in which 15% of the metabolizable energy was provided by corn starch or choice white grease. Pigs from genetic strains (genotypes) with a high, moderate, or low lean tissue content were fed the experimental diets from 126 to 253 pounds body weight. Measurements represent average values from four muscles from each carcass.

[b]Degree of paleness of pork was measured. The higher score indicates a higher degree of paleness.

[c]Data were not collected.

Furthermore, dietary fat additions improve the ability of the muscle to retain water resulting in lower exudative losses from pork during retail storage. The magnitude of the response is greatest in genetically lean pigs and in pork muscles containing the highest proportion of white muscle fibers. However, dietary fat additions, especially unsaturated fat sources, have been reported to lower the firmness and texture scores of pork products (Table 3). Furthermore, susceptibility of the pork to oxidation and the associated losses in pigmentation and development of off-flavors during storage are increased in pigs fed highly unsaturated fat sources.

Table 3. Influence of dietary fat concentration and composition on pork quality.

	Added Dietary Fat		
Criteria	None	Saturated Fat	Unsaturated Fat
Intramuscular fat composition, %			
Saturated	40	32	25
Unsaturated	59	68	75
Physical characteristics[b]			
Color	3.4	3.6	2.8
Firmness	4.3	3.7	2.6
Texture	4.2	3.5	3.2
Oiliness	4.7	4.2	2.5
Off-flavors, %	19.1	18.8	28.6

[a]Adapted from Miller et al. (1990).
[b]Five-point scale (5=red, firm, fine, no oil).

The amount and type of dietary fat consumed also has been shown to influence the immune status of monogastric animals, although this relationship has not been studied extensively in pigs. As greater amounts of fat are absorbed, the ability of laboratory animals to remove foreign substances (i.e., bacteria) from the body seems to be partially inhibited. On the other hand, the synthesis of key immune regulatory compounds (i.e., prostaglandins) are influenced by the type of fat consumed. Omega-6 fatty acids, such as linoleic acid which is present in high concentrations in vegetable oil, may stimulate the immune system by serving as a precursor for synthesis of a key immune regulatory compound. In contrast, omega-3 fatty acids, such as eicosepentamine acid present in fish oils, minimize or inhibit the immune system. In animals experiencing moderate levels of antigen exposure, greater stimulation of the immune system via dietary addition of certain types of fat (i.e., high linoleic acid) may be desirable. In contrast, the additional priming of the immune system by feeding specific fatty acids may result in an excess response of the immune system when the animal experiences a high or acute level of antigen exposure. For example, the susceptibility of laboratory

animals to toxic shock associated with endotoxin exposure is increased and reduced, respectively, in animals receiving high concentrations of omega-6 (Table 4) and omega-3 fatty acids prior to acute endotoxin exposure. However, based on initial results, the growth response of pigs (13 to 60 pounds) experiencing a moderate or high level of chronic antigen exposure to dietary fat source are similar (Table 5).

Table 4. Influence of dietary fat additions on the survival and immune response of rats administered endotoxin.

	Energy Source[a]		
Criteria	Glucose	MCT	Corn-Soy Oil
Survival, %	50	50	20
Lymphocyte blastogenesis[b]	17,603	27,301	660
Phagocytosis rate[b]	10.3	12.1	.9

[a]Adapted from Hoki et al. (1991, 1992). Glucose, MCT (medium chain triglycerides), and corn-soy oil (high omega-6 fatty acids) administered intravenously to rats previously exposed to endotoxins.
[b]Measures of the ability of immune system components to mount an immune response to an antigen (endotoxin).

Table 5. Growth responses to dietary fat additions in pigs experiencing a moderate or high level of chronic antigen exposure.[a]

	Antigen	Dietary Energy Source	
Criteria	Exposure	Starch	Fat
Feed intake, lb/day	Mod	1.96	1.75
	High	1.59	1.50
Body gain, lb/day	Mod	1.13	1.17
	High	.91	.96
Feed/gain	Mod	1.73	1.50
	High	1.75	1.56

[a]Adapted from Stahly et al. (1996). Pigs (13 to 60 pounds body weight) were self-fed a corn-soybean meal mix containing 15% of the dietary metabolizable energy provided as corn starch or fat (choice white grease or corn oil).

Dietary fat additions also influence the amount and characteristics of the various waste products produced by pigs. Dietary fat additions have been shown to reduce aerial concentrations of fine dust particles present in enclosed swine buildings. Potentially, this response could be associated with

lower endotoxin concentrations in the air. Furthermore, a smaller proportion of the energy in the diet is lost from the body as heat. Fecal dry matter excretion also should be reduced slightly. This response is due in part to the higher concentration of energy per gram of absorbed fat versus that of absorbed carbohydrates. Fat also tends to slow digesta passage which is associated with slight improvements in protein and carbohydrate digestibility and thus slight reductions in nitrogen and fiber excretion. Dietary additions of fat, particularly saturated fats, lower phosphorus digestibility and thus potentially increase phosphorus excretion slightly.

In conclusion, the impact of dietary fat additions on the rate, efficiency, and composition of growth in pigs needs to be addressed to evaluate the economic value of dietary fat source for growing pigs. The energetic value of fat versus starchy feedstuffs is greatest when the biological status of the animal allows the energy source to be used predominately for body fat deposition. The impact of dietary fat on pork quality, immune system status, and, to a minimal degree, waste production also needs to be addressed when evaluating the amount and type of fat to be fed.

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The Energy Cost of Illness in Swine

Dr. Rodney W. Johnson, Assistant Professor of Integrative Biology, Department of Animal Sciences, University of Illinois, Urbana, Illinois

Summary

Dirty, less hygienic environments increase the level of immunological stress and depress growth and performance of pigs. In response to challenge by bacterial or viral pathogens, the pig's immune system responds by secreting cytokines. These molecules which promote inflammation were originally described for their ability to orchestrate the immune response against the infectious pathogen. It is now recognized that cytokines also act on other targets outside of the immune system. The cytokines released by activated macrophages have been found to alter the metabolism of carbohydrate, fat and protein substrates, regulate certain endocrine secretions, and reduce food intake. In short, many findings converge to suggest that a major component of the growth inhibition observed in immunologically challenged pigs is mediated by pro-inflammatory cytokines. The goal of this short paper is to provide an integrated view of how immunological stress through the secretion of cytokines depresses growth in pigs.

Introduction

Disease and growth have long been two of the most important issues in pig research. Although animal scientists and husbandmen alike have long recognized that sick pigs fail to eat and therefore grow, only recently have they begun to understand the relationship between growth and disease. Disruption of a pig's internal milieu by infection or injury threaten its integrity and require immunological, behavioral and physiological responses so that a relative homeostatic state may be achieved. These responses may be subtle, as is probably the case for pigs with a subclinical, chronic, low-grade infection. Other instances, however, require a more extensive response. In any case, there is a reduction in food intake and a deliberate shift in the partitioning of dietary nutrients away from lean muscle accretion towards metabolic responses that support the immune system. It makes sense that the pig would readily sacrifice growth in order to contend against pathogens that may otherwise lead to disease and perhaps death. This complex which is commonly referred to as immunological stress (Klasing and Johnstone, 1991), also accelerates breakdown of muscle protein. Thus, the shift in the balance between anabolic and catabolic processes forms the basis for impaired growth and feed utilization in pigs subjected to infectious and noninfectious agents.

Immunological Stress Re-Partitions Nutrients

Dirty, less hygienic environments increase the level of immunological stress and depress growth and performance. The concept that immunological stress diverts nutrients from productive processes (e.g., lean tissue accretion and lactation) is not new. More than 20 years ago Bruce Young devised a graphic scheme depicting the partitioning of dietary energy (Figure 1; see Curtis, 1983). It shows that as the energy required to maintain body integrity and combat stress increases, the energy available for production decreases. What is important in the area of immunological stress and growth is the newly acquired appreciation for how the pig's immune system communicates with other physiological systems to orchestrate this shift in priorities.

The old idea was that the reduction in feed intake, growth and efficiency seen in immunologically challenged pigs were caused directly by infectious pathogens which disabled or impaired cellular function. Although still valid to some extent, we have proposed that an immunological mechanism is at least partially responsible for this phenomenon (Kelley et al., 1994). To fully appreciate why or how the immune system regulates growth, one must first understand how cells of the immune system behave when challenged by a pathogen. As shown in Figure 2, when exposed to lipopolysaccharide (LPS) which is a molecule found on the surface of gram-negative bacteria (e.g., *Escherichia coli*), the macrophage responds by secreting at least three cytokines; interleukin-1 (IL-1), interleukin-6 (IL-6) and tumor necrosis factor-α (TNF-α) (Figure 2). These cytokines up-

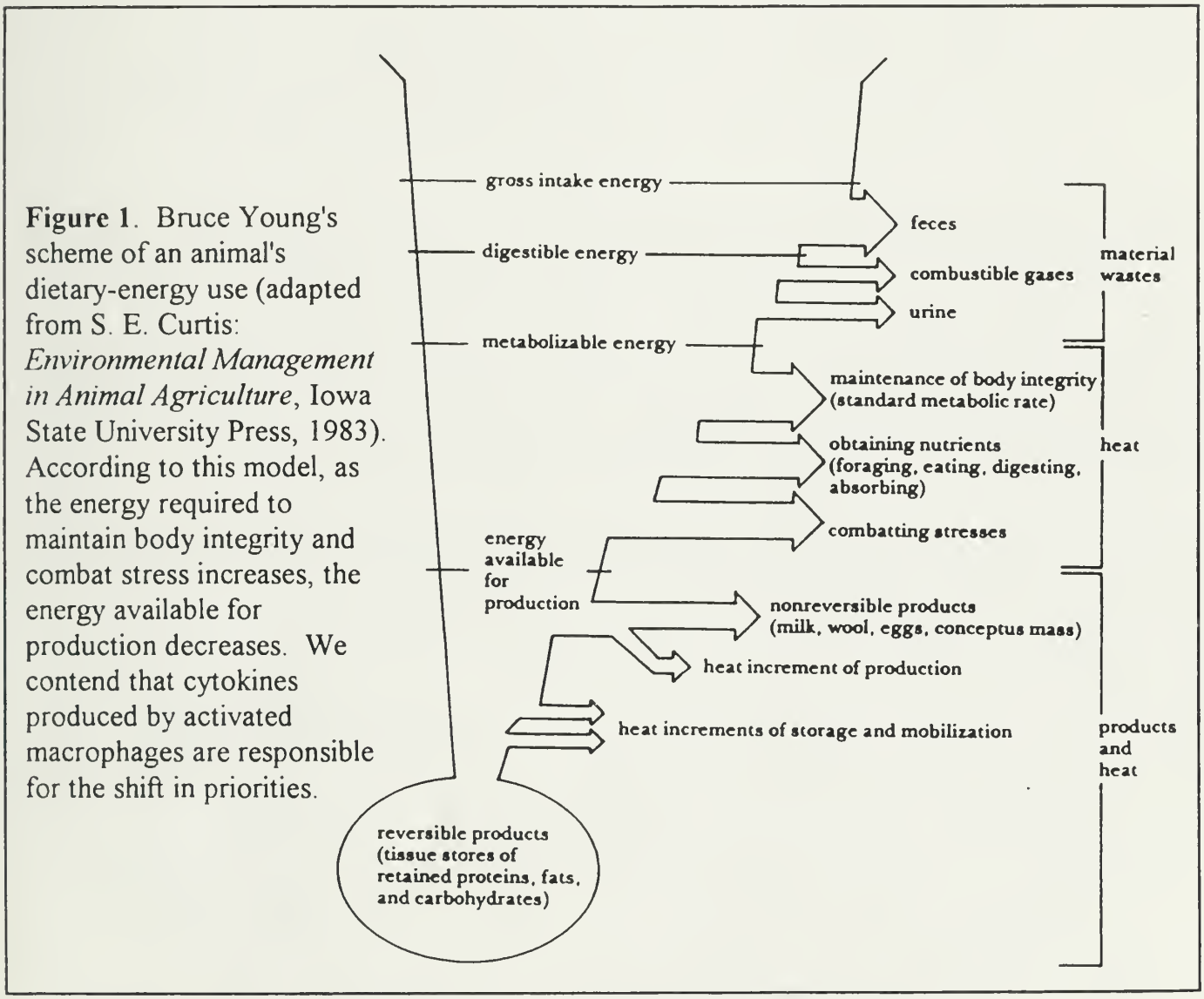

Figure 1. Bruce Young's scheme of an animal's dietary-energy use (adapted from S. E. Curtis: *Environmental Management in Animal Agriculture*, Iowa State University Press, 1983). According to this model, as the energy required to maintain body integrity and combat stress increases, the energy available for production decreases. We contend that cytokines produced by activated macrophages are responsible for the shift in priorities.

regulate the immune response (Figure 2) so that the host can better contend against the invading pathogen. Interestingly, these pro-inflammatory molecules also act "outside" the immune system. In essence they are important messengers used by the immune system to inform the rest of the body of an ongoing challenge. This cytokine signal from the immune system re-organizes the animal's priorities, and metabolic changes that serve the immune system at the expense of growth ensue. An example of how this re-organization might influence protein metabolism is described below.

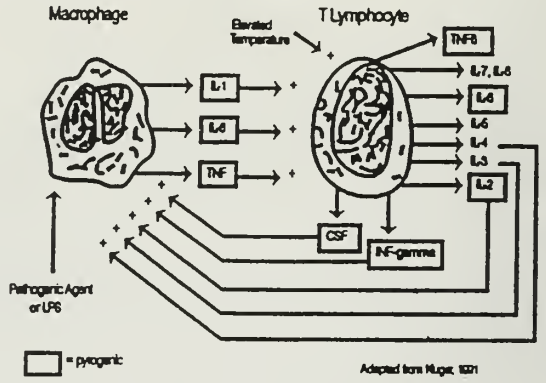

Figure 2. The macrophage produces cytokines which modulate other immune cells. These cytokines can also have profound metabolic effects which inhibit growth (adapted from Kluger, 1991).

How Does the Immune System Antagonize Growth?

Cytokines inhibit growth in many ways and some of these are summarized in Figure 3. It should be noted that the current understanding of the metabolic effects of cytokines is largely based on studies conducted in small rodent animals. However, several recent studies in pigs indicate similarities between species and therefore suggest that many of the well-described effects of cytokines in rodents can be extended to pigs. With this precautionary note in mind, upon examination of the effects of pro-inflammatory cytokines on protein metabolism, it is easy to appreciate the broad implications of immunological stress for pig growth.

First, it is evident that a pig experiencing a "high level" of immunological stress has a lower motivation for food and eats less than a pig experiencing a lower level of immune stimulation. This is evidenced by the numerous studies showing that pigs kept under all-in, all-out management eat more, grow faster and are more efficient at converting feed to gain compared to pigs kept under continuous flow management. Of course, the efficacy of all in, all out management to improve growth performance of pigs is attributed to the ability to appropriately disinfect the environment between groups of pigs. In doing so, immunological stress is reduced. It is important to note that the pro-inflammatory cytokines are well known for their ability to reduce appetite and alter the utilization of protein, fat and carbohydrate substrates.

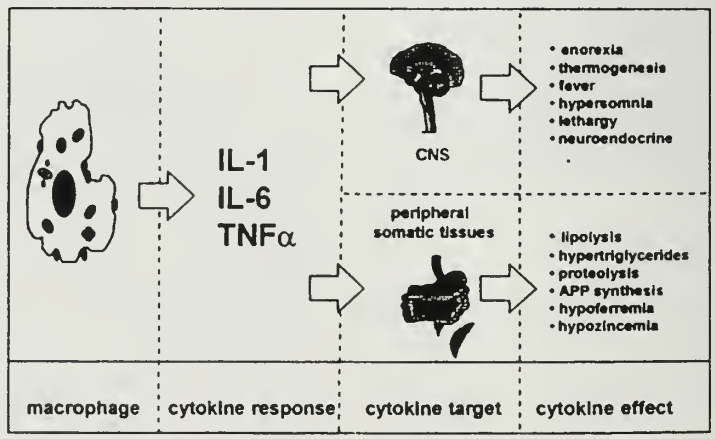

Figure 3. Pro-inflammatory cytokines act on different physiological systems and have effects that are likely to inhibit growth (from Johnson, submitted).

Second, during the inflammatory response there is an increase in synthesis by the liver of acute phase proteins. Synthesis of some acute phase proteins may increase several 100-fold. It has been estimated in humans that during an inflammatory response the acute phase proteins increase in concentration by about 850 mg protein/kg body weight (Reeds et al., 1994). The synthesis of acute phase proteins is an important component of the inflammatory response since some proteins both activate complement to lyse bacteria and opsonize bacteria to help the immune system clear it. Nonetheless, this increased demand for hepatic protein synthesis can impose a substantial "tax" on growth. For instance, if the pig is consuming less protein (i.e., its appetite is reduced) but must increase hepatic synthesis of acute phase proteins, from where are the amino acids which fuel this process derived? Of the amino acids used in protein synthesis, at least 60% are derived from body protein degradation. And because skeletal muscle protein represents the largest available pool of amino acids, it seems reasonable to postulate that this is the principal source. Indeed, by comparing the amino acid composition of the acute phase proteins to that of skeletal muscle protein, Reeds et al. (1994) estimated that to provide enough phenylalanine (the limiting amino acid for acute phase protein synthesis) to synthesize 850 mg of acute phase protein, 1980 mg of skeletal muscle protein would have to be degraded. Because many of the other amino acids liberated by degradation of skeletal muscle are in excess, they are excreted. Again, it is important to note that the pro-inflammatory cytokines not only stimulate hepatic acute phase protein synthesis, but also induce degradation of skeletal muscle protein. Thus, the cytokines are part of a network which seems to inherently link muscle protein synthesis/degradation with hepatic acute phase protein synthesis.

From a practical standpoint this may explain why in a recent study conducted by Tim Stahly's group at Iowa State University, pigs kept under a management scheme that presumably provided fewer immunological challenges (e.g., Medicated Early Weaning) consumed more feed, grew faster, and retained more nitrogen for proteineous tissue growth (Williams et al., 1993). In this study, pigs maintained in an environment that presumably imposed a high degree of immunological stimulation, also had high plasma levels of the acute phase protein, α_1-acid glycoprotein. From this and other studies it is simple to see why the emerging view is that sickness in pigs, manifesting as reduced feed intake and lowered lean muscle growth, is the result of increased biosynthesis of certain cytokines. However, the evidence for such a connection is only now emerging.

To more directly address this issue, in a recent study we injected pigs with lipopolysaccharide to induce immunological stress so that the relationship between plasma cytokines and protein and lipid metabolism could be evaluated (Webel et al., in press). Some of the results of this study are summarized in Figure 4. It is interesting to note that only after the marked increase in TNF-α, IL-6 and cortisol (a catabolic hormone released in response to stress), was there an increase in plasma urea nitrogen. Because the pigs were fasted

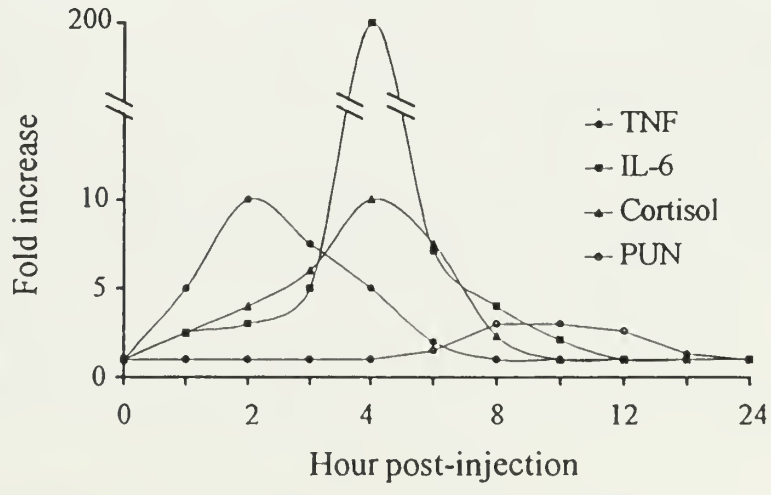

Figure 4. Several effects of LPS in pigs (from Webel et al., in press).

beginning 12 hours prior to injection, it seems reasonable to postulate that the 3-fold increase in plasma urea nitrogen was the end result of muscle protein degradation. Thus, these results corroborate the idea that secretion of pro-inflammatory cytokines increases muscle protein degradation. Whether these same concepts can be used to explain the chronic depression in feed intake and growth in seemingly healthy pigs is an important question.

Implications

The best strategy for inhibiting the costly effects of increased cytokine activity is obvious: reduce disease and immunological stress. Maintaining a clean hygienic environment and incorporating "growth-promoting" levels of antibiotics into the diet are common practices which help control this complex. Unfortunately, even pigs reared under the best management experience some degree of immunological stress which prevents them from growing at their true genetic potential. Because this depression in growth and efficiency is probably mediated by cytokines, understanding how these products of the immune system alter metabolic processes is important. This type of information is critically needed to design diets and management schemes which improve growth and performance of pigs experiencing farm-level immunological stress.

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Net Energy for Growth in Pigs: Application to Low Protein, Animo Acid Supplemented Diets

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Introduction

The cost of feed is at least 50% of the total cost of pig meat production with the energy component representing the greatest proportion. Therefore, from a practical point of view, it is important to estimate precisely the energy value of feeds, either for least-cost formulation purposes or for adapting feed supply to energy requirements of animals. Evaluation of energy content of pig feeds is usually based on their digestible (DE) or metabolizable (ME) energy contents. However, the closest estimate of the « true » energy value of a feed is given by its net energy (NE) content which takes into account the metabolic utilization of ME. Therefore, NE systems have been proposed. In addition, NE is the only system in which energy requirements and diet energy values are expressed on a same basis which should be independent of the feed.

The most recent NE systems were established from measurements carried out in fattening (Schiemann et al., 1972) or in growing (Just, 1982a) pigs fed mainly cereal-based diets; they used the Weende fractionation method of organic matter. These systems have been used in many countries, especially in Northern Europe. However, according to changes in the pig industry (more by-products in feed formulation, modern lean-type pigs, progress in analytical procedures, ...) and some limitations in the above systems, it appeared as necessary to reconsider these proposals (Noblet et al., 1993a, 1994a and 1994b ; CVB, 1994 ; Noblet, 1996).

The increased concentration of pig herds and the environment constraints (i.e. reduction of soil and water pollution by nitrogen from manure) have forced to propose new feeding strategies for growing pigs. The most efficient technique consists in reducing the amount of nitrogen intake and keeping the amino acids supplies adequate for meeting the animals requirements. Phase-feeding systems combined with the use of low protein diets supplemented with industrial amino acids have therefore been proposed. Under an ideal situation, nitrogen output can be reduced by about 50%, as compared to conventional feeding strategies (Dourmad et al., 1992 ; Bourdon et al., 1995)

The first purpose of this paper is to present available energy systems (DE, ME and NE) for evaluation of pig feeds, with more emphasis on NE systems. The second purpose is to consider the consequences of lowering the level of protein in pig diets on their energy value, according to energy system. Some biochemical aspects of protein utilization and results of

growth trials will also be considered. Information on methodological aspects has been given by Noblet (1996).

Energy Utilization of Pig Feeds

Digestive Utilization

For most pig diets, the digestibility coefficient of energy (DCe or DE:gross energy ratio) varies between 70 and 90% for most pig diets. The variations are associated with differences in fecal digestibility of the nutrients constituting organic matter. However, most of the variation of DCe is associated with the presence of fiber which is less digestible than other nutrients (below 50%) and reduces the apparent fecal digestibility of crude protein and fat (Noblet and Pérez, 1993). In addition, the digestive utilization of fiber is variable with its botanical origin (Chabeauti et al., 1991). An example of the effect of fiber level on DCe of compound feeds in growing pigs is given in Table 1. Such an equation should not be applied to raw materials where specific relationships are to be used (Noblet and Henry, 1993).

Table 1. Effect of diet composition[1] (g/kg dry matter) on digestibility coefficient of energy (DCe, %) and ME/DE ratio (%) and efficiency of utilization of ME for NE in growing pigs (k_g, %).

EQUATION	RSD	REFERENCE
DCe = 102.1 - 0.171 x Ash - 0.167 x CF	2.2	Noblet and Pérez, 1993
DCe = 101.3 - 0.095 x Ash - 0.095 x NDF	1.7	Noblet and Pérez, 1993
ME/DE = 100.3 - 0.021 x CP	0.5	Noblet and Pérez, 1993
k_g = 74.7 + 0.036 x EE + 0.009 x ST - 0.023 x CP - 0.026 x ADF	1.2	Noblet et al., 1994a

[1] CF: Crude Fiber, CP: crude protein, NDF: Neutral Detergent Fiber, ADL: Acid Detergent Lignin; EE: ether extract, ST: starch, ADF: Acid Detergent Fiber.

Literature studies indicate that DCe is also affected by factors not related to the diet itself. In growing pigs, DCe increases with body weight (BW) (Noblet and Shi, 1994), with larger differences for high fiber feeds. The largest effect of BW is observed when adult sows and growing pigs are compared: digestibility coefficients are superior in all cases for the sows, the difference being greater with fibrous diets or ingredients (Fernandez et al., 1986 ; Noblet and Shi, 1993). In addition, the difference also depends on the origin of fiber. For instance, the values measured for wheat bran and corn gluten feed in growing pigs represented 90 and 70% of the value recorded in sows, respectively (Noblet and Bourdon, 1997).

ME:DE ratio

The ME content of a feed is the difference between DE and energy losses in urine and gases (mainly as methane). In growing pigs, average energy lost in methane is equivalent to 0.4% of DE intake (Noblet et al., 1994a). In sows fed at maintenance level, methane production

represents a much higher proportion of DE intake (1.5 vs 0.4% in growing pigs , Noblet and Shi, 1993)

Energy lost in urine represents a variable percentage of DE since urinary energy is highly dependent on the amount of nitrogen in urine; the urinary nitrogen will mainly depend on the amount of digestible protein and, therefore, on the crude protein (CP) content of the diet Consequently, the ME:DE ratio is linearly related to dietary protein content (Tables 1 and 2) In most situations, the ME:DE ratio of complete feeds is relatively constant and equivalent to about 0.96. However, that mean value cannot be applied to single feed ingredients (Shi and Noblet, 1993)

Metabolic Utilization of ME

NE is defined as ME minus heat increment associated with metabolic utilization of ME and also to the energy cost of ingestion and digestion. The ratio between NE and ME (or k , k_g for NE in growing pigs) corresponds to the efficiency of utilization of ME for NE. Apart from variations due to the final utilization of ME (protein gain vs fat gain vs milk production vs ...), k varies according to the chemical characteristics of the feed since nutrients (oses, amino acids, long-chain fatty acids or volatile fatty acids) are not used with similar efficiencies. In studies conducted with growing pigs, k_g was increased when fat and starch contents were higher and reduced when protein or fiber contents were enhanced (Table 1). Similar trends were observed in adult sows fed at maintenance energy level (Noblet et al., 1993a). The variations of k_g are due to differences in efficiencies of ME utilization of nutrients: 90, 82, 73, 58 and 58% when ME was provided by digestible ether extract, starch, sugars, digestible crude protein and digestible fiber, respectively. Corresponding efficiencies of DE of nutrients for NE were 90, 82, 72, 50 and 54% (Noblet et al., 1994a).

Metabolic Utilization of Energy from Protein

In Table 2, the different steps of energy utilization, expressed as a function of digestible nutrient contents, are presented. The equations indicate that most of the variation in energy losses occurring in the DE to ME step are related to the utilization of digestible crude protein (DCP) in connection with the excretion of nitrogen as urea . From the coefficients of DCP or catabolized DCP (DCPc) in the DE and ME prediction equations, the energy loss can be estimated as about .7 to .8 kcal per g of DCPc. Comparable estimates can be obtained from the studies of Schiemann et al. (1972) in near-maturity pigs and Noblet et al. (1993) in adult sows at maintenance energy level (.8 and .7 kcal/g of DCPc, respectively). Even the N in urine is not only as urea, it can be noticed that these values are close to the energy content of urea (.87 kcal/g N x 6.25). The ME value of DCPc is then equivalent to about 4.7 kcal/g.

In the ME to NE step, energy losses as heat increment in growing pigs concern all nutrients : about 2.0, 1.0, .75 and 1.2 kcal per g of DCP, digestible ether extract, starch and digestible fiber, respectively (Table 2). According to the same approach, it was 1.6 kcal per g of DCP in maintenance adult sows (Noblet et al., 1993a) or growing pigs (Just, 1982b) and 2.3 kcal per g of DCP in near-maturity pigs (Schiemann et al., 1972). In all studies, the heat increment due to the metabolic utilization of DCP is significantly higher than for starch or ether extract.

Table 2. Prediction equations of DE, ME and NE (kcal/kg of dry matter) in growing pigs from digestible nutrient contents (g/kg of dry matter) (from measurements on 61 diets ; Noblet et al., 1994)

Equation[1]	RSD	Reference[2]
DE = 5.46 x DCP + 9.29 x DEE + 2.74 x DCF + 4.19 x ST + 4.05 x Sugars + 4.38 x DRes	21	1
ME = 4.77 x DCP + 9.42 x DEE + 2.29 x DCF + 4.19 x ST + 3.98 x Sugars + 4.14 x DRes	27	1
NEg2 = 2.69 x DCP + 8.36 x DEE + 0.00 x DCF + 3.44 x ST + 2.89 x (DRes + Sugars)	52	2
ME = .975 x DE - .69 x DCPc		
DEc = 5.40 x DCPc + 9.24 x DEE + 2.68 x DCF + 4.16 x ST + 4.03 x Sugars + 4.37 x DRes	21	3
MEc = 4.60 x DCPc + 9.23 x DEE + 2.10 x DCF + 4.08 x ST + 3.89 x Sugars + 4.05 x DRes	30	3
ME/DE = 100.1 - .0200 x CP	.6	3
ME/DE = 98.7 - .0164 x DCP	.7	3
ME/DE = 97.5 - .0187 x DCPc	.7	3

[1] CP, DCP, DEE, DCF, ST, Sugars for crude protein, digestible crude protein, digestible ether extract, digestible crude fiber, starch and sugars, respectively ; DCP corresponds to catabolized DCP (or N in urine x 6.25) ; DEc (or MEc) are equal to DE (or ME) minus retained energy as protein ; DRes is equal to digestible organic matter minus the other digestible nutrients considered in the equation ; ME includes energy losses as methane.

[2] 1 : Noblet, 1996 ; 2 : Noblet et al. (1994a) ; 3 : J. Noblet, unpublished

The heat increment of DCP as measured in the above studies corresponds to the combination of heat increments of DCP for protein gain and DCP for maintenance (ATP production) and, in some instances, for lipid synthesis. Biochemical approaches indicate that, as compared with glucose or fat, about 20% more ME is required for ATP formation when it is supplied by protein (Krebs, 1964 ; Armstrong, 1969 ; Schulz, 1975). It must also be mentioned that increased protein supply is associated with a higher protein turnover (Reeds et al., 1981) and an increased mass of visceral organs (Noblet et al., 1987) with subsequently enhanced heat production. As mentioned before, the catabolism of protein is associated with urea synthesis whose energy content is considered in the DE to ME step ; but urea synthesis also requires energy which is dissipated as heat. According to the estimates of Buttery and Boorman (1976), it would be equivalent to about .6 kcal per g of DCP (on the basis of about 5 ATP per mole of urea). Finally, when DCP or amino acids are used for protein deposition, additional energy as ATP for peptide bond and associated increased body protein turnover is required. The estimates of additional energy for protein deposition are quite variable ; .6 to .7 kcal per kcal retained which is equivalent to an energetic efficiency of 60% (so-called k_p) can be suggested. This value is remarkably comparable to the efficiency of utilization of ME of DCP for NE.

Overall, there are many factors which explain the high rate of heat production when energy is supplied by DCP or when the amount of DCP in the diet is increased. But, further studies are

required to evaluate their respective contributions. In addition, the coefficient affected to DCP in the NE equations has been obtained with diets whose protein levels increased from conventional to excessive levels. The situation of low protein diets supplemented with synthetic amino acids has not been extensively considered. The metabolic studies of Fuller et al. (1987), Noblet et al. (1987) and Moehn and Susenbeth (1995) would confirm the expected reduced heat loss with low protein and amino acids supplemented diets in growing pigs. Growth trials (see Tables 6 to 9) also confirm the same hypothesis.

From the available information (Table 2), it is proposed that the NE value of 1 g of DCP is about 2.7 kcal (or 2.4 kcal per g of CP if the DC of CP is 90%) while the estimated NE content of 1 g of starch is 3.4 kcal; starch is supposed to be 100% digestible. Consequently, the substitution of 1 g of protein by one g of starch should increase the NE value of the diet by about 1 kcal; on a ME basis, the energy value would hardly be changed and it would be decreased on a DE basis (minus .7 kcal/g). In practical terms, for a diet containing 2200 kcal NE per kg, the DE content would be reduced by about .30% and the NE value would be increased by about .45% for each 1% reduction of the CP level and its replacement by starch. Ewan (1991) suggested that NE value of a diet was increased by about .6% for each 1 percent reduction of the CP level. Addition of both estimates (.45% plus .30%, i.e. .75%) gives an indication of the additional DE to supply in order to maintain the same NE supply when starch is replaced by protein in the diet. In a similar approach, Noblet et al. (1987) suggested a slightly higher figure (1%) from results of an experiment conducted in young growing pigs.

Prediction of Net Energy Value

All published NE systems combine the utilization of ME for maintenance and for growth (Just, 1982; Noblet et al., 1994a and 1994b) or for fattening (Schiemann et al., 1972) by assuming similar efficiencies for maintenance and energy retention. Equations proposed by Noblet et al. (1993c) can be used to predict NE value of feeds in a maintenance situation. One important aspect is that NE value is directly dependent on the estimate of fasting heat production used in the calculation; the practical consequence is that absolute NE values obtained under different measurement conditions or with different hypotheses cannot be compared.

In studies conducted at INRA, each diet was measured for its chemical composition, DE, ME, and digestible nutrient contents with the objective of using these data as predictors of NE content. Different linear regression models were tested. But, for practical application, such regression equations should use easily available criteria, either from feeding tables or at the laboratory level (i.e. from accurate and not expensive analyses). The most important NE prediction equations we obtained on 61 diets fed to 45-50 kg Large White boars are presented in Table 3. They can be applied to both single feedstuffs and mixed diets. The first one (NE_g2) is based on digestible nutrient contents which can be calculated from chemical characteristics and digestibility coefficients of the different fractions. Digestibility coefficients in most feedstuffs are available in Dutch (CVB, 1993) or German or Danish feeding tables; it can be assumed that starch is 100% digestible. The two other equations (NE_g4 and NE_g7) take into account the DE or ME contents and some chemical characteristics. They can also be applied from information available in feeding tables which indicate DE or ME contents of most feedstuffs used in pig diets formulation. Reliable information on digestibility of energy or of nutrients is then necessary for prediction of NE content of pig feeds.

Table 3. Equations for prediction of net energy in pig feeds (kcal/kg dry matter; composition as g per kg of dry matter) (from Noblet et al., 1994a).

EQUATION[1]	RSD,%
$NE_g2 = 2.69 \times DCP + 8.36 \times DEE + 3.44 \times ST + 0.00 \times DCF + 2.89 \times DRes$	2.0
$NE_g4 = 0.703 \times DE - .97 \times CP + 1.58 \times EE - .98 \times CF + .47 \times ST$	1.7
$NE_g7 = 0.730 \times ME - .67 \times CP + 1.31 \times EE - .97 \times CF + .37 \times ST$	1.6

[1] DCP, DEE, DCF, ST, CP, EE and CF correspond to digestible crude protein, digestible ether extract, digestible crude fiber, starch, crude protein, ether extract and crude fiber, respectively; DRes is the difference between digestible organic matter and the other digestible nutrients considered in the equation.

The studies we conducted in heavier pigs or in adult sows indicate that the equations obtained in young growing pigs (Table 3) are applicable at all stages of pig production (Noblet, 1996) In the case of adult sows fed at maintenance, the measured NE_m value is higher than the calculated NE_g; but the difference between NE_m and NE_g is not explained by any chemical characteristic of feeds. This means that the equations proposed in Table 3 and based on DE, ME or digestible nutrient contents are able to determine an acceptable hierarchy between feeds when they are used in a maintenance situation. The superiority of NE_m over NE_g will be taken into account in the calculation of requirements. But, as shown above, the digestibility coefficients of energy or chemical constituents vary according to body weight of animals with major differences between adult sows and growing pigs (especially for high fibre feeds). Net energy values should then be different for both stages.

Comparison of DE, ME and NE Systems

From the equations reported in Tables 1, 2 and 3, it is obvious that the hierarchy between feeds obtained in the DE or ME systems will vary in the NE system according to their specific chemical composition. Since NE represents the best estimate of the "true" energy value of a feed, the energy value of protein or fibrous feeds is overestimated when expressed on a DE (or ME) basis. On the other hand, fat or starch sources are underestimated in a DE system. These conclusions are more clearly demonstrated in Tables 4 and 5.

Table 4. Energy values of some ingredients in DE, ME and NE systems (Noblet et al., 1993b and 1994a)[1].

	DE	ME	NE
'Diet', Mcal/kg DM[2]	3.99	3.87	2.92
As a percentage of 'diet' energy content:			
Wheat	97	97	99
Corn	95	94	101
Tapioca	95	96	104
Soybean meal	98	94	75
Peas	97	97	92
Animal fat	179	182	222

[1] DE and ME correspond to measured energy values and NE is the mean NE value obtained from equations NE_g2, NE_g4 and NE_g7 (Table 3).

[2] Diet corresponds to the combination of 81.5% wheat, 15% soybean meal and 3.5% animal fat.

Table 5 Relative energy values of ingredients in DE and NE systems (Noblet et al., 1994b)

System	DE	NE	NE/DE (x100)
Ingredients, % of basal diet[1]			
Corn starch	115	131	82
Rapeseed oil	237	300	90
Sucrose	104	114	78
Protein mixture[2]	147	133	64
Fiber mixture[3]	55	44	57

[1] Basal diet was a mixture of cereals, soybean meal and MV

[2] 50% casein and 50% extracted soybean protein

[3] 25% wheat bran, 25% soybean hulls, 25% sugar beet pulps and 25% ground wheat straw

These tables clearly demonstrate that the hierarchy between feeds is dependent on the energy system, the biggest differences being observed for ingredients whose chemical composition is quite different from that of standard diets (fat sources and protein- and/or fiber-rich ingredients). Results in least-cost formulation will therefore depend on the energy system. Unpublished results show that diets have lower protein contents when formulated on a NE concept than on a DE basis and a subsequent higher supplementation of synthetic amino acids.

Performance and Utilization of Energy in Growing Pigs Fed Low Protein Diets

The effect of reducing the protein level in diets for growing pig has been studied in many experiments but under very variable conditions. If we limit our purpose to experiments in which essential amino acids supply across diets was kept constant, correctly balanced and above requirements for optimal growth, the number of experiments becomes considerably lower. The main difficulties in interpreting data are then differences in feeding strategy (ad libitum vs restricted feeding) or the absence of information on protein and energy value of diets or on body composition of pigs. Most important and synthetic results of some recent experiments are presented in Tables 6 to 9.

Table 6. Effect of dietary crude protein level on performance of growing pigs (Valaja et al., 1993)[1]

Dietary CP, %	16.3	14.8	13.2	11.7	Diet effect
ADG, g/d	871	881	890	883	NS
Mcal ME/kg gain	9.85	9.89	9.82	10.03	NS
Backfat thickness, mm	24.4	25.0	26.3	27.3	P<.001

[1] All diets supplied essential amino acids above requirements ; 30 pigs per treatment (half castrated males and half females ; group housing ; feeding scale according to BW) ; between 25 and 105 kg BW ; ME content was estimated from feeding tables

The effect of lowering the dietary CP level (at constant supply of essential amino acids) on voluntary feed intake (VFI) is not quite clear and results are contradictory. The differences in response are probably related to factors such as genotype or sex, nature of ingredients, sub-limiting or excessive levels of some amino acids and environmental conditions. However, the general trend would be a slight increase of VFI with the reduction of CP level. In most

experiments conducted under ad libitum feeding or even restricted feeding (on a DE or ME scale), the growth was not affected and the carcasses at slaughter contained more fat and less lean when the CP level is reduced (Tables 6 and 7). This situation is quite logical under ad libitum feeding since the trend is an over-consumption of energy. If carcasses are fatter when low CP diets are fed at similar DE or ME intakes, this means that more energy is retained in the body and also more energy is available from the diet (Tables 6 and 7). In comparable experiments but at controlled NE intakes, CP level affected neither growth of the animals nor body composition at slaughter (Tables 8 and 9) ; in addition, the feed conversion ratio was affected by CP level when expressed on a DE basis and independent on CP level when expressed on a NE basis (Table 8). In the previous experiments (Tables 6 and 7), the feed conversion ratio, expressed on a DE or ME basis, was not affected by CP level while an increased fat content in the carcass suggests an increased energy requirement per unit of BW gain.

Table 7. Effect of dietary crude protein level on performance of growing pigs (Cromwell et al., 1996 and G. Cromwell, personal communication)[1]

Dietary CP, %	16.8-15.0-13.6	14.9-13.0-11.6	13.3-11.5-10.1
ADG, g/d	721	735	730
Mcal ME/kg gain	9.90	9.99	10.01
Backfat thickness, mm	26.4[a]	27.9[ab]	29.7[b]

[1] Three successive diets were used over the growing, developing and finishing periods ; at each period, the supply of essential amino acids was above requirements in all treatments ; between 20 and 111 kg BW ; ME was estimated from feeding tables. Thirty six pigs per treatment (group housing and ad libitum feeding).

Table 8. Effect of dietary crude protein level on performance of growing pigs (Dourmad et al., 1993)[1]

Dietary CP, %	17.8	15.5	13.6	Diet effect
ADG, g/d	846	857	852	NS
Feed conversion ratio				
Mcal DE/kg	9.13a	8.94b	8.88b	P<.05
Mcal NE/kg	6.57	6.56	6.59	NS
Carcass fat content, %	19.1	18.6	19.3	NS

[1] Between 29 and 103 kg BW ; all diets supplied the same amounts of essential amino acids ; 40 pigs per treatment (castrated males and females from 2 genotypes) ; DE content was measured ; pigs were fed restrictively according to a NE scale ; NE was calculated from DE and chemical characteristics (Noblet et al., 1994). Animals were housed and fed Individually.

The combination of these results indicates that the energy value of low protein diets is underestimated and/or the energy value of conventional diets is overestimated when it is expressed on a DE basis. These conclusions are quite consistent with the differences in the relative energy values of different feeds in DE and NE systems (Tables 4 and 5) and the high heat production and energy loss as urea associated with the utilization of excessive DCP (Table 2).

Table 9. Effect of dietary crude protein level on performance of growing pigs (Bourdon et al., 1995)[1]

Dietary CP, %	17.0	18.0-14.5	15.0-12.0	Diet effect
ADG, g/d	847	855	843	NS
Mcal NE/kg gain	6.16	6.11	6.17	NS
Carcass fat content	23.9	22.3	23.1	NS

[1] Nine pigs per treatment ; between 25 and 101 kg ; in the 17.0% CP treatment, the same diet was fed over the total experiment ; in the two other treatments, two diets were mixed in variable proportions (phase feeding system) over the experiment : from 100 to 0% of the higher protein diet from the beginning to the end of the experiment and vice versa for the lower protein diet ; essential amino acids were above requirements in all treatments. Energy was supplied according to a NE scale (estimated from DE measurements on diets). Animals were housed and fed individually.

Conclusions

Theoretically, energy requirements of animals and energy values of feeds can be expressed on the same basis when the NE concept is used for both of them. Furthermore, NE value of a feed should be a better predictor of the growth response of pigs than DE value, since it is closer to the « true » energy value of feeds. These assumptions are illustrated in Tables 8 and 9 in the case of diets with variable CP contents. The same conclusion was given for diets with variable fat contents (Noblet, 1996). In addition, difficulties in the interpretation of increased fatness of carcasses of pigs fed low protein diets (or also high fat diets) are quite reduced when differences in NE intakes are considered Net energy systems are therefore highly preferable in such situations.

However, when changing from DE (or ME) to NE systems and using low protein diets, attention should be paid to the reduction of amino-acids levels and the subsequent risk of sub-limiting available amino-acids supplies to the pigs. Consequently, it is highly suggested to adopt an accurate protein evaluation system (available or digestible amino-acids) when a NE system is used and/or CP level is reduced, in order to adapt feed composition more precisely to requirements and growth potential of the pig. An other consequence is that the utilization of low CP diets may result in fatter carcasses in connection with the slight over-consumption of feed and its higher NE value. Reduction of CP level with sufficient supplies of essential amino acids should then be combined with strategies for limiting energy intakes, especially with animals depositing rather large amounts of fat (castrates).

It must also be stated that prediction of net energy value of pig feeds depend directly on their digestible (or metabolizable) energy or digestible nutrients contents. These latter quantities depend firstly on dietary characteristics of the feed, but they are also affected by (bio)technological treatments, animal factors and interactions between these factors and feed composition. Improvements in the prediction of energy value of pig feeds will therefore come mainly from a better knowledge of factors of variation of energy and nutrients digestibility. In the above paragraphs, we have particularly insisted on the differences between adult sows and growing pigs.

One major objective in the reduction of CP level in growing pigs or sows diets is to reduce the nitrogen output from pig production. This can be significantly achieved with good knowledge

of amino acids and energy requirements of animals and accurate estimation of the nutritional value of feeds (available amino acids, net energy). An other objective in reducing the CP level (and/or increasing the fat content) might be to decrease the amount of heat which is dissipated by the animals. A potentially high heat production can represent a limiting factor in pigs kept under hot climatic conditions or with a limited heat tolerance ; they will then react by a lower VFI and subsequent reduced performance. The use of low CP and/or high fat diets might then be an attractive solution to reduce heat stress (Lopez et al. 1994). Such strategies deserve further experimental studies and confirmation.

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Effect of Genotype on Energy/Feed Intake

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Young pigs between weaning and slaughter and lactating females are generally fed ad libitum on the majority of commercial units in the US and, therefore, a critical factor determining their performance levels is their voluntary feed intake. For the growing-finishing animal, which is the focus of this paper, a combination of its feed intake level and lean growth rate largely dictate the nutritional program for optimal performance. Lean growth rates determine animal requirements for nutrients and feed intake potential sets the nutrient density required in the diet to meet these requirements.

It is widely recognized that both lean growth rates and feed intake or appetite levels are under genetic control, although genetic variation in lean growth has generally received much more attention than genotype differences in appetite. This paper sets out to review the information available on genetic variation in appetite, its association with lean growth and other performance parameters and also examine the likely impact of current and future swine selection programs and practices on genetic change in feed intake.

Genetic Variation in Feed Intake

Genetic differences in feed intake, as well as in other growth performance and carcass characteristics, can be found between breeds, between distinct genetic lines within a breed, and between individuals within a line. The world swine research literature has an abundance of papers of breed comparisons for feed intake, growth performance, carcass characteristics and other traits. However, in a large number of these studies only a limited number of breeds have been compared, perhaps two or three in most situations, these studies have often been based upon a limited sample of animals from each breed, have been carried out in many different countries and under widely different production systems, and are often dated and, therefore, of historical interest only.

One of the most extensive genetic comparisons carried out in the US in recent years is the Terminal Line Evaluation carried out by the National Pork Producers Council. This evaluation compared a number of the purebreds that are used in the US as well as some different seedstock sources for a wide range of traits. The feed intake and growth performance of the different sire lines that were evaluated are presented in Table 1. The pigs used in the comparison were produced on commercial units with sire lines being mated to a range of female types that could be considered representative of the commercial industry. These data show substantial variation between genetic source for daily feed intake (from 2.48 to 2.68 kg/day) as well as for other traits.

A breed that has received considerable attention in Europe is the Duroc which is of interest because of its high intramuscular fat levels and its potential impact on eating quality. In comparison with European white breeds and lines and under European production conditions, the Duroc has generally been shown to have a higher feed intake and growth rate but to be fatter. This, however, is not substantiated by the data in Table 1 which suggests that the Spot and Berkshire sires gave the highest feed intakes whilst the Large White population had the highest growth rates. This illustrates that the results of any genotype comparison will largely be determined by the sample of a particular population that is evaluated and which other populations are included in the comparison.

Another breed that is being used in the US and elsewhere is the Pietrain, which is generally characterized by its short muscular carcass and high carcass lean contents. This breed, generally, has poor reproductive performance and is used only as a sire line. There is little if any current data available in the scientific literature relating to the feed intake and growth performance of the Pietrain relative to other breeds. Historical evidence from Europe would characterize this breed as having a relatively low feed intake and growth rate compared to breeds such as the Large White, Landrace, and Duroc. Most studies have tended to show that the lean growth rate of the Pietrain is similar to the white breeds and, thus, the high carcass lean content of the Pietrain results from reduced fat deposition rates. There is no up-to-date comparison of the Pietrain with US breeds. In a recently completed study at the University of Illinois, a line that was originally based on the Pietrain (line A) was compared to two commercial sire lines (lines B and C). Line B was a halothane carrier line and produced both carrier and negative progeny. The sire lines were mated to a commercial crossbred female line and the progeny were compared. The results of this comparison (Table 2) illustrate the lower feed intake and growth rate for Line A compared to the others, which showed similar performance levels.

Gu et al. (1991) compared five genetic lines that represented a range of genotypes available to the US industry and again showed a wide range in feed intake and other growth traits (Table 3), confirming the variation that exists between commercial populations under US conditions. An association can be seen in these data between lean growth rate and feed intake, with Genotype 5 having the highest lean growth rate but on of the lowest intake and Genotype 4 having low lean gain and high intake levels. To illustrate the way in which feed intake and lean growth rate interact to determine diet composition, the data for lines 4 and 5 have been used to calculate protein requirements and the dietary nutrient concentrations required to meet these requirements and these calculations are presented in Table 4.

In actual fact, there is probably as much if not more variation in feed intake between different genetic lines within the same breed as there is between different breeds. This is illustrated in Table 5, where the results of a study which compared similar commercial product lines from four of the major British breeding companies is presented. Three of the companies are currently involved in supplying breeding stock to the US industry. The range in performance levels was high, amounting to 10% of the mean for feed intake, 14 and 16% of the mean for daily gain and feed conversion ratio, respectively, and a staggering 23% of the mean for lean growth rate. The

means for feed intake and lean growth rate for the individual company populations are presented in Table 6. An interesting feature of this data is that the population (Company J) with the highest lean growth rate had a low feed intake and the company with the lowest lean growth rate had a relatively high feed intake (Company K). These data and those of Gu et al. (1991) suggest a negative association between lean growth rate and appetite.

Genetic Association Between Feed Intake and Lean Growth Rate

Is the genetic association between feed intake and lean growth potential always negative ? Do leaner pigs always grow slower than fatter pigs ? These are two common questions the basis of which lies in the circumstantial evidence found in the results of genotype comparisons such as those summarized in Tables 3 and 6. The answer to both these questions is no. The genetic relationship between appetite and lean growth can be positive as well as negative and leaner genotypes can grow faster than fatter genotypes. The relationship between intake and lean growth depends largely on the testing and selection program under which the genetic lines has been developed and particularly on the combination of selection criteria and feeding regime employed.

The genetic relationships between growth rate, feed efficiency, and carcass lean content on the one hand and feed intake on the other are not fixed and vary with testing environment. The statistic that is used as measure of the degree of the genetic relationship between traits is the "Genetic Correlation", which estimates of the genetic change in one trait consequent upon a genetic change in another. The size and even the direction of the genetic correlation between two traits can vary between testing environments. For example, the genetic correlation between growth rate and carcass lean content is negative under ad libitum feeding but positive under restricted feeding regimes. The impact of selection for increased growth rate on carcass fat levels would, therefore, be in exactly the opposite direction for the two feeding regimes. Selection for faster growing pigs under ad libitum feeding would result in genetically fatter pigs whereas under restricted feeding faster growing animals would be genetically leaner. This illustrates the critical interaction of selection criteria (which traits are selected for) and testing regime (how the traits are measured) in determining the outcome of a selection program.

Historically, pigs have been selected for improved growth and carcass characteristics using a selection index which has combined the traits of growth rate, feed efficiency, and carcass lean content into a single value which is used as the basis of selection decisions. The emphasis placed on these three traits in an index has largely been determined by their relative economic importance, which obviously varies between specific situations and, particularly, from country to country. However, in the vast majority of swine industries feed efficiency is of greatest economic importance, followed generally by carcass lean content and then growth rate. Therefore, traditional selection indexes placed more emphasis on feed efficiency and carcass leaness than on growth rate. When such indexes are used in combination with testing pigs using an ad libitum feeding regime the genetic response obtained is to select pigs with reduced appetites that consequently deposit less fat and have improved feed efficiency. This type of approach has been

termed selection for lean tissue feed efficiency (Fowler et al., 1976).

Evidence for reductions in feed intake as a result of selection for improved lean tissue feed efficiency can be found in a number of studies including that of Smith et al. (1991). In this study, a population of Large Whites were selected under ad libitum feeding for approximately seven generations using a selection index which included feed efficiency, backfat thickness, and growth rate, with the relative weights on these being approximately 80, 15, and 5% respectively. The responses to this selection program were measured using an unselected control herd and amounted to significant improvements in backfat thickness and feed efficiency, little change in growth rate, and a reduction in feed intake. The feed intake curves for boars and gilts from the selection line and control line boars from this experiment are illustrated in Figure 1. The reduction in feed intake for selection line boars relative to controls was proportionately constant (approximately 10% of the control line mean) across the weight range studied (30 to 90 kg).

Reduced feed intake is of much greater relative importance at lighter weights where intake may limit growth performance. This is illustrated by the data of Campbell et al. (1983) who measured protein deposition rates in pigs between 20 and 45 kg across a range of feeding levels spanning very low to ad libitum. The results of this study are presented in Figure 2 and show that protein gain of gilts plateaued at feed intakes below ad libitum whereas there was no plateau in the response of males. Entire males have higher lean growth rates than gilts and feed intake was limiting lean growth in the males in this experiment. In fact, low feed intake may limit protein gain at heavier weights as illustrated by the data of Campbell and Taverner (1988). These authors investigated the influence of dietary energy intake on protein growth between 45 and 90 kg live weight in boars from two strains of pig (A and B) and castrates from strain B (Figure 3). Strain B boars and castrates showed a plateau to protein gain but there was no evidence of any upper limit in strain A boars, suggesting that the genetic ceiling to protein gain was above the intake limit for this genotype.

Current and Future Genetic Change in Feed Intake

Selection for reduced feed intakes as a mechanism for reducing carcass fat levels and improving feed efficiency resulted in the development of lines of pigs that can be grown to slaughter weight using ad libitum feeding without becoming excessively fat. However, if selection continues down this response curve, low feed intakes will eventually limit animal performance and this problem is likely to be encountered first in the young growing animal and in the lactating female, particularly in her first parity. In fact, intakes may be reduced to such an extent as to limit any future genetic response to selection.

In addition, the substantial genetic improvements in backfat thickness and carcass leanness have produced populations with levels approaching an optimum and further selection to reduce these will be counterproductive. Therefore, most current selection programs emphasize improving lean growth rates (Fowler et al, 1976) and achieve improvements in feed efficiency as a correlated response, rather than selecting for this trait directly. When the selection for lean growth rate is

carried out under ad libitum feeding then improvements in growth rate and feed efficiency and increases in feed intake are expected.

The interaction between selection criteria and feeding regime have been investigated in a large scale selection experiment that has recently been carried out in the United Kingdom (Cameron et al. 1994). The results of four generations of selection for either lean growth rate or lean tissue feed conversion efficiency under ad libitum feeding are presented in Table 8. Selection for lean tissue feed conversion ratio produced little change in growth rate, a reduction in feed intake, and a consequent improvement in backfat thickness and feed efficiency. In contrast, selection for lean growth rates achieved improvements in feed efficiency through increased growth rate with a correlated increase in feed intake and little change in backfat thickness. It is obvious from these results that there is no fixed genetic relationship between feed intake and lean growth and that these will be changing over time and in a way that is largely dependant on the selection program used.

What changes are occurring in feed intake in commercial populations ? McLaren (1996) has stated that feed intake levels are increasing in PIC sire and dam lines (Table 8). However, there is little or no data available from other sources to evaluate changes in other commercial populations.

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Table 1. Terminal sire evaluation results (NPPC, 1995)

	Feed Intake, kg/d	Weight gain, kg/d	Feed conversion ratio
Berkshire	2.66	0.836	3.07
Danbred HD	2.48	0.803	2.88
Duroc	2.61	0.824	2.91
Hampshire	2.56	0.784	2.92
NGT Large White	2.52	0.900	2.94
NE SPF Duroc	2.62	0.824	2.89
Newsham Hybrid	2.51	0.833	2.83
Spot	2.68	0.830	3.14
Yorkshire	2.53	0.830	2.93

Table 2. Comparison of commercial sire lines

Sire line	A	B	B	C
Halothane status	Carrier	Negative	Carrier	Negative
Daily feed intake(kg)	2.37	2.82	2.72	2.79
Daily gain (kg)	0.885	1.049	1.057	1.082
Gain:feed	0.38	0.37	0.39	0.39

Miller et al., unpublished (1996)

Table 3. Genotype effects on lean growth and feed intake

Genotype	Feed intake, kg/d	Daily gain, g/d	Lean growth rate, g/d
1	3.15	916	329
2	3.02	924	361
3	3.06	1010	390
4	3.24	1001	332
5	3.03	1017	393

Gu et al. (1991)

Table 4. Feed formulation as affected by genotype, lean growth and feed intake in finishing pigs.

Genotype	1	2
Lean growth, g/d	332	393
Feed intake, Kg/d	3.24	3.03
Protein accretion, g/d *	102	121
Total lysine requirement g/d**	15.3	18.5
Lysine in diet, g/kg	4.72	6.11
CP % in a corn-SBM diet	11.73	13.62

* protein accretion = lean growth/3.25

** 15 g of total lysine/ 100 g of protein lean gain.

Table 5. Range in performance among UK breeding companies

	Mean	Range
Feed intake, kg/d	2.16	2.07-2.29
Daily gain, g/d	842	774-890
Feed/gain	2.59	2.45-2.87
Carcass lean, %	55.2	51.6-58.2
Lean growth, g/d	365	315-400

MLC (1988)

Table 6. Lean growth rates and feed intake in UK breeding companies

Company	J	K	L	M
Lean growth rate, g/d	400	315	356	388
Feed intake, Kg/d	2.09	2.20	2.29	2.07

MLC (1988)

Table 7. Response to 4 generations of selection for lean growth or lean feed conversion ratio under Ad libitum feeding.

	Lean growth rate	Lean feed conversion ratio
ADG, g	+52	-7
ADFI, g	+80	-56
Feed:Gain	-0.052	-0.05
Average backfat thickness, mm	-0.08	-1.32

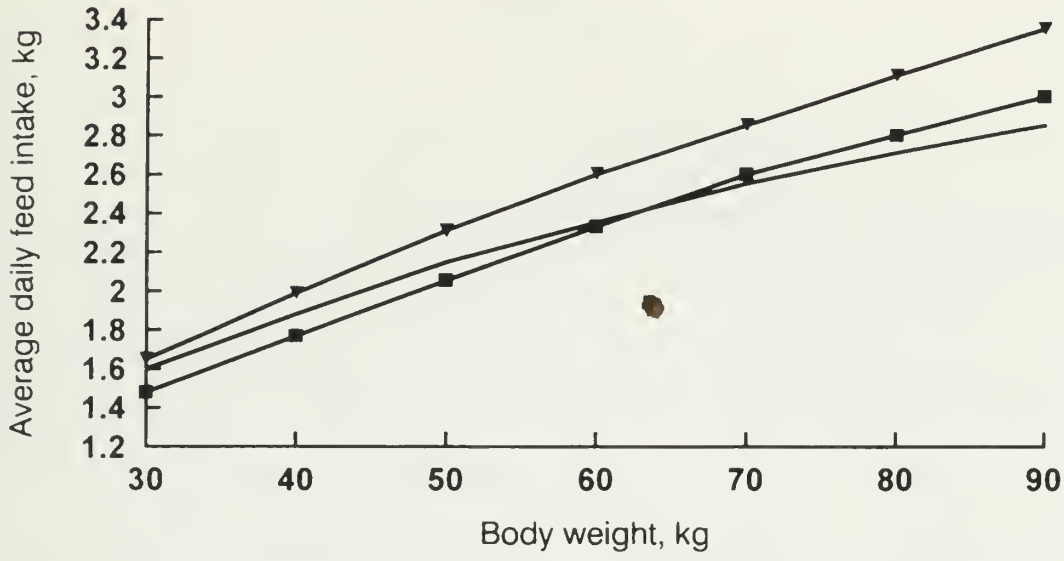
Cameron et al. (1994)

Table 8. Estimated genetic change in average daily feed intake in PIC lines, 1991 to 1995

	Change, kg/year
Dam lines	+0.033
Sire lines	+0.018

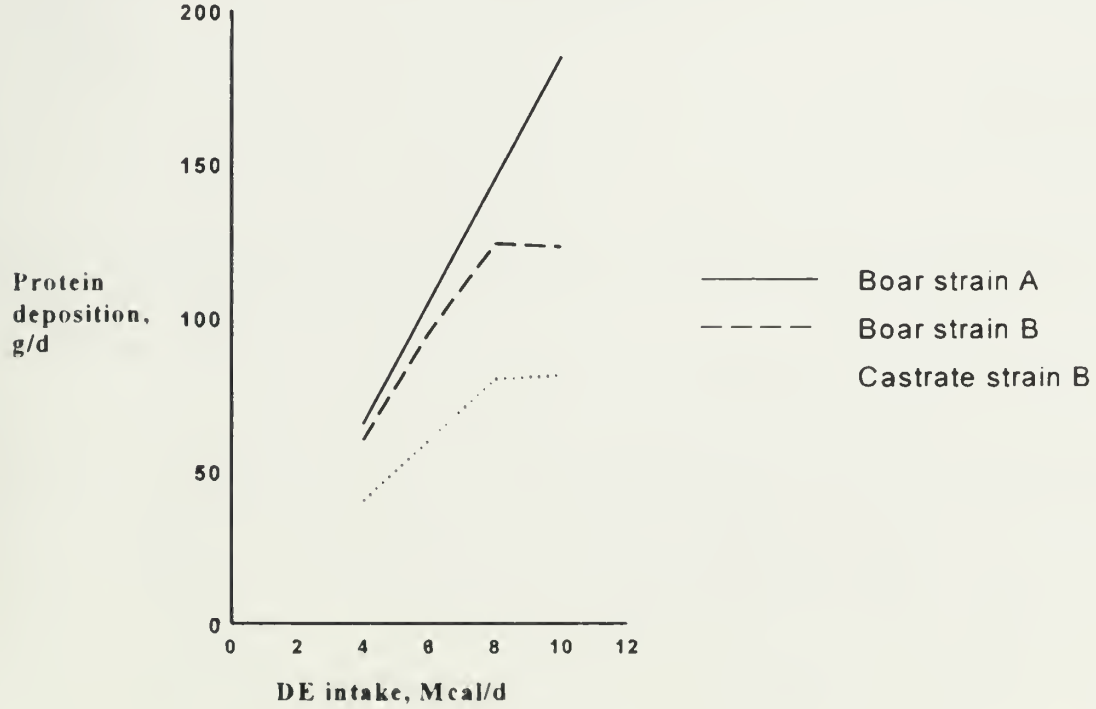
McLaren, (1996)

Figure 1. Feed intake curves for selected and control line pigs



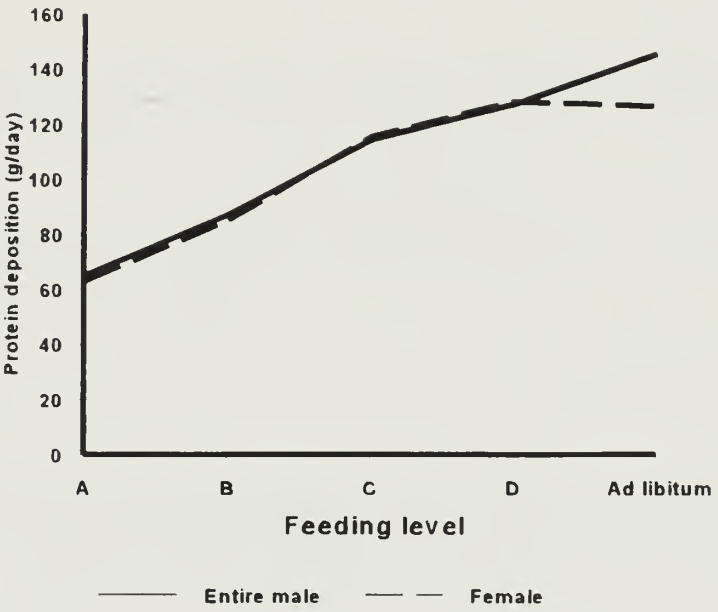
Smith et al . (1991)

Figure 2. The relationship between energy intake and rate of protein deposition for two strains of intact boars and for castrated male pigs growing from 45 to 90 kg live weight.



Campbell and Taverner (1988).

Figure 3. Effect of sex and feeding level on the rate of deposition of protein of pigs growing from 20 to 45 kg of body weight.



Campbell et al. (1983)

Role of the Central Nervous System in Energy Balance

J. Lee Beverly

Energy balance is regulated by the central nervous system (CNS). The CNS coordinates the provision of energy and specific nutrients with the prevailing endocrine state and nutriture to support the metabolic needs of the animal. The appropriate internal environment for maintenance, physical activity, growth, and reproduction is maintained by constant adjustments in energy intake and energy expenditure. Neural, humoral, and metabolic signals inform the CNS of the body's internal environment and are integrated with information on conditions in the external environment (e.g. feed availability, social conditions, temperature, etc.). Unfortunately, there has been little work in swine evaluating the role of the CNS in energy balance and it's role in growth and performance. This review will summarize the role of the CNS in energy expenditure and feed intake and some of the factors that influence the two, as demonstrated in other monogastric animals.

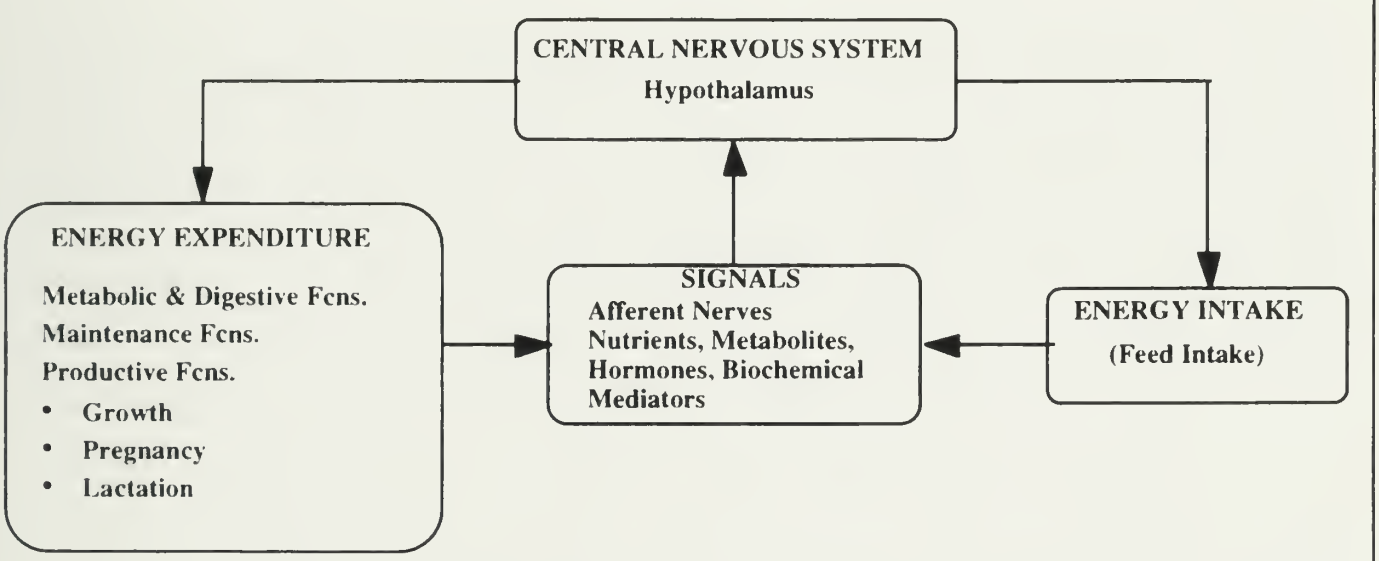


Figure 1. Signals reflecting the two components of energy balance, expenditure and intake, allow coordination by the hypothalamus .

The brain area that initiates the hormonal, metabolic and behavioral systems regulating basal metabolism and energy balance is the hypothalamus. The hypothalamus coordinates neuroendocrine influences, behaviors, and activity of both branches of the autonomic nervous system to maintain caloric homeostasis. The neuroendocrine influences alone impact stress responses, mobilization of energy nutrients, metabolic rate, growth of lean tissue, and some reproductive processes. The resulting hormonal profiles provide a background on which behaviors and the relative activity of the sympathetic and parasympathetic nervous systems contribute to the existing endocrine compliment. The consequences to changes in endocrine status and behavior tend to be of longer duration than the immediate responses to activation of the Autonomic Nervous System.

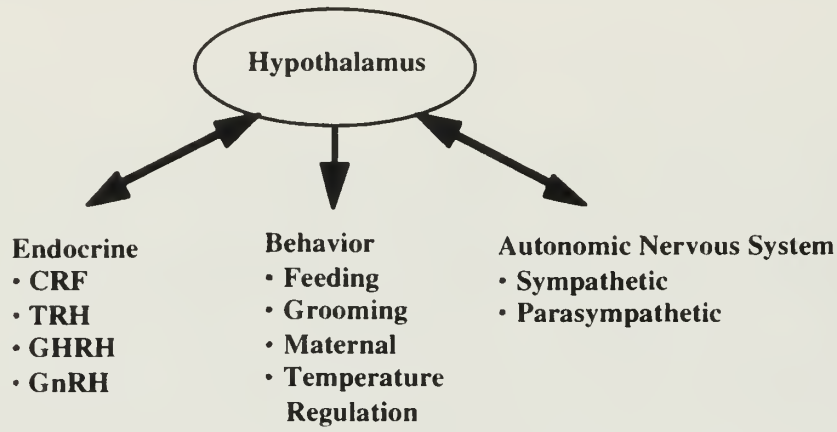


Figure 2. Role of the hypothalamus in factors influencing energy balance.

Endocrine

Within the hypothalamus specific peptides (or "releasing factors") are synthesized to regulate the release of corticothyrotropin, somatotropin and gonadotropin hormones from the anterior pituitary. Corticotropin releasing factor (CRF) stimulates the release of adrenocorticotropic hormone (ACTH) into the circulation which stimulates the release of the corticoids from the adrenal gland, such as cortisol. Thyrotropin releasing hormone (TRH) stimulates the release of thyroid-stimulating hormone (TSH) which induces release of the thyroid hormones, including thyroxine. Growth hormone releasing factor (GRF) induces growth hormone release and, indirectly influences the production of somatomeidans, such as insulin-like growth factors (IGFs) from the liver. The release of the gonadotropins, follicle-stimulating hormone (FSH) and leutinizing hormone (LH), from the anterior pituitary are regulated by gonadotropin-releasing hormone (GnRH). Localization of the cell bodies of the neurons varies among the various releasing factors. Both CRF and TRH are found in the paraventricular nucleus (PVN), GRF is found in the anterior hypothalamus and the arcuate nucleus (ARC), and GnRH is found in the lateral hypothalamus (LHA). Axons from the cell bodies extend to the median eminence where the peptides are released into the portal circulation of the pituitary. Direct innervation of the posterior pituitary by the hypothalamus provides for the release of the neural hormones, vassopressin and oxytocin. These two hormones, having key roles in fluid balance, are released from nerve endings that extend from the supraoptic and paraventricular nuclei of the hypothalamus.

A feature of the neuroendocrine system in the hypothalamus is negative feedback by the hormones to reduce further release of their releasing factors. This feature exemplifies how circulating factors, in this case hormones, influence events in the CNS. The impact of altering activity of the releasing factors may go beyond their effects on the release of hormones into the circulation. Each of the releasing factors exert influences within the hypothalamus that compliment the physiological responses to the hormones they release and allows greater coordination of energy and nutrient availability with their metabolism. When administered into the hypothalamus CRF inhibits feeding, reduces gastric acid secretion and gastric emptying, and increases the activity in parts of the sympathetic nervous system to induce a thermogenic response and to mobilize glucose and free fatty acids (Steffens et al., 1990). These responses are independent of an effect on ACTH release and are consistent with the role of the adrenocorticoid hormones in stress. Food intake is increased in response to TRH administration (Morley, 1980), consistent with the effect of the thyroid hormones to increase metabolic rate. When administered centrally GRF stimulates a preference for

dietary protein (Dickson and Vaccarino, 1990), which would benefit the increased protein synthesis in the periphery by growth hormone.

Behavior

The importance of the hypothalamus in behaviors, especially those associated with the condition of the internal environment has been widely studied. Connection with limbic and cortical areas allows the hypothalamus to integrate information from the external environment and emotions with information on the status of the internal environment. Behaviors directly affecting energy balance are feeding, time spent grooming, maternal behaviors, and temperature regulation. The role of the hypothalamus in feed intake will be discussed in greater length below. Grooming's effects on health and the impact of maternal behavior on progeny survival indirectly influence energy balance. Maternal behaviors often relate to utilization of resources by the sow for perinatal support and may be facilitated by prolactin. The hypothalamus is also involved in sexual behavior of both male and female animals, via it's connections with the limbic system, and is responsive to alterations in circulating estrogen and testosterone concentrations.

Maintenance of body temperature is another function of the hypothalamus that impacts energy balance. Heat production, a consequence of metabolism, feed intake, and physical activity, and heat dissipation, via conduction and respiration, are influenced by the hypothalamus. Internal body temperature is monitored by temperature-sensitive cells in the anterior hypothalamus and initiate changes in autonomic nervous system activity, endocrine secretions, and behavior to aid thermoregulation. In cold environments the autonomic nervous system facilitates shivering and vasoconstriction, TSH secretion is increased to effect an increase in metabolic rate, and feed intake and physical activity are increased. In response to warm environments, vasodilation and panting are initiated by the autonomic nervous system, TSH secretion is decreased, and food intake and physical activity are reduced. The pyrogenic response to infection is mediated via the preoptic area (POA) of the anterior hypothalamus. Activation of the POA occurs in response to various biochemical mediators, such as interleukin-1 and interleukin-6, that are released during disease.

Autonomic Nervous System

It is through the activity of the two branches of the autonomic nervous system, the parasympathetic (i.e. vagus) and sympathetic nervous systems, that the hypothalamus has immediate impact on energy balance by creating conditions favoring anabolism (parasympathetic) or catabolism (sympathetic). Both branches are widely distributed throughout the internal organs, have both motor and sensory function, and, in general, act in a reciprocal fashion. Within the hypothalamus, the VMH and PVN mediate activity of parts of the sympathetic nervous system while the LHA mediates activity of the parasympathetic nervous system. These brain areas are reciprically innervated, providing for coordination of activity of the two autonomic branches. Through these brain areas, peripheral energy metabolism is both monitored and regulated. Neural elements sensitive to the concentration of both glucose and fatty acids are found in the VMH and LHA. In response to glucose, glucose-responsive cells in the VMH decrease their firing rate and firing rate of glucose-sensitive cells in the LHA is increased. The opposite occurs in the presence of fatty acids. Activity of specific neural systems in the VMH are increased in response to acute alterations in circulating levels of some nutrients (Beverly et al, 1995). Stimulation of these neural pathways in the VMH activates the sympathetic nervous system, and depresses the parasympathetic nervous system, which, because of increased plasma concentrations of epinephrine, norepinpehrine, glucagon, and corticosteroid , results in increased circulating levels of glucose and free fatty acids. Increased neurochemical activity in the LHA is associated with an increase in the parasympathetic nervous system, and decrease in sympathetic nervous system, and increased insulin secretion and a

decrease in glucose and free fatty acid concentrations in the circulation. In response to endogenous or environmental stressors sympathetic activity is increased and plasma levels of catabolic hormones and calorigenic nutrients are increased.

Feed Intake

The amount of feed consumed is influenced by a variety of variables reflecting the animals internal state and the environment. The form in which changes in feed intake occur in response to any single variable or combination of variables can differ widely. The animal's physiological state is often manifested as changes in selection among feedstuffs or in their pattern of feeding. Analysis of feeding behavior affords a window to the internal state of an animal and it's interaction with external stimuli. As such, there is an opportunity for non-invasive monitoring of factors that influence the well-being and performance of the animal.

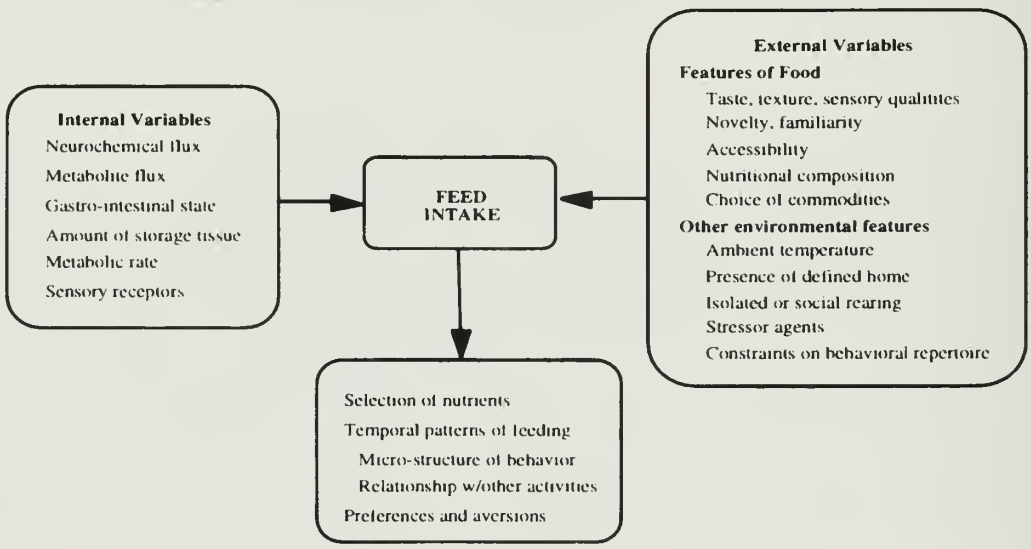


Figure 3. Internal and external variables affecting feed intake.

External factors that affect feed intake include features of the food itself. Sensory qualities can impact acceptability of a feed. The greater intake of diet containing spray dried porcine protein by weanling pigs has been attributed to the sensory qualities of the diet (Ermer et al. 1994). Taste is also used to identify a feed and contributes to the development of learned aversion to a diet (Houpt et al., 1979). Familiarity with a diet, it's accessibility, and choice among feedstuffs also influence intake of a given feed. Most animals exhibit neophobia when confronted with a new diet, especially when in a new environment. Decreasing competition for feeder access by increasing the number of feeders within a pen increased food intake of piglets (Appleby et al. 1992). When offered a choice between two diets that differ in the amount of protein growing pigs select between the two diets to arrive at a constant protein intake (Kryiazakis et al., 1990). Pigs are also able to select against inappropriate diets, as intake of diets containing an imbalance in the indispensable amino acids is reduced (Robinson, 1975).

Features of the environment also impact feed intake. Feed intake is inversely related to ambient temperature, with intake decreasing as temperature increases. This response may be related to

body size with young animals being more tolerant of higher temperatures than older animals (Forbes, 1995). Pen size and stocking density influence the level and pattern of feed intake. Intake is decreased as available space decreases and longer, less frequent meals often result from limiting space (Lindvall, 1981). In group-housed conditions, feed intake decreased as animal number within a pen was increased, independent of space per animal (Kornegay and Notter, 1984). The importance of social interaction on intake is less clear, though some impact on meal patterns is evident; eating is often initiated by the sight of other pigs eating (Hsia and Wood-Gash, 1983). A feeding pattern of shorter, more frequent meals occurs when pigs are housed individually, vs group-housed animals. (de Haer and Merks, 1992).

Feed intake is affected by the state of the internal environment as well. There has been very little work on neurochemical mechanisms that regulate feed intake, and energy balance, in swine. In other species, it is clear that changes in neurochemical pathways respond to changes in energy balance and initiate endocrine, behavioral, and autonomic responses that affect energy balance. It is likely that the same, or similar mechanisms also influence energy balance in swine. Feed intake is affected by gastrointestinal state, with capacity and sensory receptors in the gut influencing the level of intake. Diet dilution studies demonstrated increased intake as energy was diluted (Wangness and Soroka, 1978) and infusion of nutrients into the duodenum depressed oral feed intake (Gregory and Rayner, 1987). Compensation is not complete, however, as increasing digestible energy concentration in the diet usually results in increasing digestible energy intake (Henry, 1985).

Metabolite flux, as imposed by maintenance and growth, will influence feed intake. High growth rate pigs eat more than pigs selected for slower growth rate (Woltman et al., 1992). The level of feed intake appears to reflect the potential for growth. Pigs will select among diets differing in protein to provide an appropriate level of protein intake to support growth (Kyriazakis et al., 1990) and young pigs restricted in energy or protein between 9 and 16 weeks had greater feed intake and selected higher levels of protein until body composition was similar to control animals (Kyriazakis and Emmans, 1991). When treated with exogenous somatotropin, pigs have greater feed efficiency and greater carcass lean tissue (Campbell et al., 1988). These animals also tend to reduce their intake of a single diet and will consume a higher protein to energy ratio when allowed to select among diets that differ in protein content (Azain and Roberts, 1996).

In addition to the apparent effect of lean tissue growth on feed intake, the level of energy stored in adipose tissue also has an active role in energy balance. There has been a great deal of recent information on leptin, a hormone synthesized within fat cells that appears to be a signal to the CNS on energy reserves in adipose tissue. Circulating leptin correspond positively to the level of adipose mass and binds to receptors in the hypothalamus. In the hypothalamus, leptin acts to decrease feed intake and increase energy expenditure, via sympathetic nervous system-mediated thermogenesis (Campfield et al, 1995). Leptin has not been demonstrated in pigs, although it is highly conserved between mice and humans.

The utilization of energy and nutrients in a diet is often independent of the level of feed intake. Metabolizable energy intake and energy retention in carcass were similar across diets differing in protein content and lysine content; however, heat production and distribution of energy into protein and fat were quite different (Noblet et al., 1987). In pigs selected for high growth rate, more of the energy in the diet went to fat deposition than in the slow growth rate line of pigs (Woltman et al., 1992). Low protein diet supplemented with lysine resulted in increased nitrogen retention and greater overall retention of energy (Noblet et. al., 1987). Energy is spent in reducing the metabolic cost of nutrients available in excess of their need, relative to the availability of a "limiting" nutrient.

e.g. the balance of nutrients to support energy utilization for growth of lean tissues vs. fat. When somatotropin-treated pigs were provided a higher protein diet, protein intake remained adequate to increase nitrogen retention yet metabolizable energy intake was reduced and heat production was not increased (Noblet et al, 1992)

In summary, the internal environment of an animal reflects the metabolic activity supported by existing hormonal background and nutrient availability. The CNS integrates a large number of factors that reflect the state of the animal and it's environment and coordinates endocrine responses, behaviors, and activity of the autonomic nervous system to provide conditions that maintain energy balance of the animal.

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Energy and Protein Interaction of the Lactating Sow

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Introduction

Improved genetics, nutrition, housing and management systems have permitted significant increases in milk production of lactating sows. In 1972, Boomgaardt et al. (1972) studied sows that produced about 8.5 pounds of milk daily. In contrast, Johnston et al. (1993) reported daily litter growth rates of 4.86 pounds which equates to an estimated milk production of 19.5 pounds per day. In spite of these large improvements, the genetic potential for growth of nursing piglets is still not realized (Boyd et al., 1995) suggesting that improved nutritional programs that result in increased milk production will increase growth rate of nursing pigs. Heavier pigs at weaning may be of particular importance in modern production systems that implement relatively short lactations (14-18 days).

Lower than desired voluntary feed intake of lactating sows is a constant problem nagging the commercial swine industry. Many factors such as genetics, diet quality, diet composition, and environment influence voluntary feed intake of lactating sows. Time and space do not allow a complete discussion of these and their impact on the nutritional needs of the lactating sow. Our goal is to maximize feed intake of sows during lactation so that the largest possible quantity of feed is available to package the nutrients necessary for lactation.

Energy and protein, or more correctly amino acids, are the two dietary essentials needed in the greatest quantity with the exception of water. Consequently, these two classes of dietary essentials have been the focus of much research in nutrition of the lactating sow. This paper will focus on the lactation period but proper nutrition of the lactating sow begins before farrowing so that the proper stage is set for a successful lactation.

Inter-relation of Reproductive Phases

Phases of the sow's reproductive cycle are interrelated. Nutrition during one phase of the reproductive cycle influences sow performance in the subsequent phase and beyond. Therefore, a sound feeding program does not focus on nutrition during any one isolated phase of the reproductive cycle but considers the total life cycle of the sow.

Gestation feeding programs are designed to provide sufficient nutrients for development of the fetuses and associated uterine tissues, development of the mammary gland, and modest increases in maternal body weight. If given the opportunity, sows will consume feed far in excess of these needs leading to overly fat sows at farrowing. Several studies worldwide have demonstrated that increasing feed intake during gestation and the associated large increases in sow body weight depress feed intake of lactating sows (Dourmad, 1991; Revell et al., 1994; Weldon et al., 1994) (Figure 1). Low lactation feed intake can depress sow performance and shorten the sow's reproductive life.

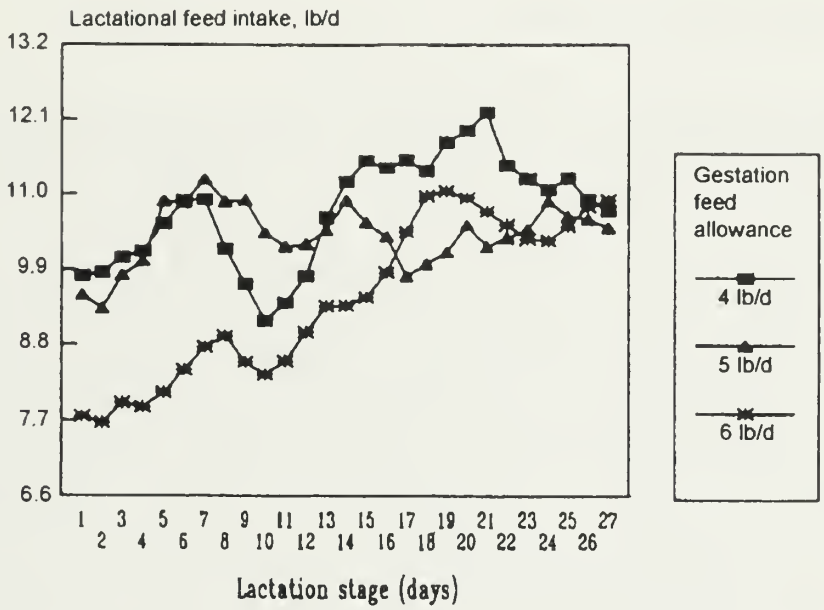

Figure 1. Effect of gestation feed intake on lactational feed intake in gilts (Dourmad, 1991)

Excessive energy intake in late gestation (after day 75) may be detrimental to subsequent milk production. Research conducted at Michigan State University suggests that energy intakes of 10.5 megacalories of metabolizable energy (ME;7.25 pounds corn-SBM diet) per day during late gestation reduces the amount of milk secreting tissue in the mammary gland compared with gilts fed 5.75 megacalories of ME (4 pounds corn-SBM diet) daily (Weldon et al., 1991). Australian researchers observed that fat gilts had fewer milk secreting cells in their mammary glands than did lean gilts (Head et al., 1991; Head and Williams, 1991). It is not clear if these differences in cell numbers will translate into differences in milk production after farrowing. In contrast to effects of elevated energy intake, increasing lysine intake from 4 to 16 grams per day (NRC recommends 8.2 grams/day) had no effect on number of milk secreting cells in the mammary gland (Kusina et al., 1995b) but did increase milk production (Kusina et al., 1995a).

Nutrient intake during lactation has profound effects on postweaning reproductive performance. Low energy (Reese et al., 1982; Johnston et al., 1989) or protein (O'Grady and Hanrahan, 1975; King and Dunkin, 1986) intake during lactation is associated with increased loss of body tissue and delayed return to postweaning estrus.

These three examples demonstrate the importance of developing a feeding program for the sow's entire reproductive cycle rather than focusing on one particular phase at the exclusion of others. Lactation is the most challenging phase of the reproductive cycle from a nutritional viewpoint. Consequently, this phase has been the subject of many experiments and will be the focus for the remainder of this paper.

Energy and Protein Needs in Lactation

Interactive effects of energy and protein. MacLean (1968) observed that sows weaned in thin body condition experienced a delayed return to postweaning estrus. This increased incidence of suboptimal reproductive performance in thin sows was referred to as the "Thin Sow Syndrome". Producers and researchers mistakenly believed that the thin condition at weaning was due to excessive mobilization of body fat throughout lactation and that increasing energy intake would correct the problem. However, Brendemuhl et al. (1987) reported that sows fed high energy, low protein diets during lactation lost similar total body weight but less backfat than sows fed low energy, high protein diets. Thus, composition of weight loss may vary depending on which dietary essential, energy or protein, is deficient and which tissue, fat or muscle, is mobilized. Furthermore, about 79% of the lysine that is present in milk proteins is derived from the diet in multiparous sows (Koehler et al., 1996). Consequently, the remaining 20% of lysine present in milk proteins must be derived from endogenous sources. These studies demonstrate that body proteins in muscle and other tissues are an important source of amino acids and energy for the lactating sow.

The sow's ability to mobilize fat or muscle tissue suggests that one cannot consider the energy and amino acid content of diets separately. Work conducted at the University of Minnesota (Tokach et al., 1992) with primiparous sows demonstrated that under relatively high energy intake the lysine requirement for maximal milk production was 45 grams per day or higher while under low energy intake the lysine requirement was only about 27 grams per day (Figure 2). In the low energy intake scenario, lysine intake above 27 grams per day did not elicit increased milk production presumably because available energy was limiting. So, the "correct" answer for the lysine requirement of the sows in this study would be 27 or 45+ grams per day depending on the sow's voluntary energy intake.

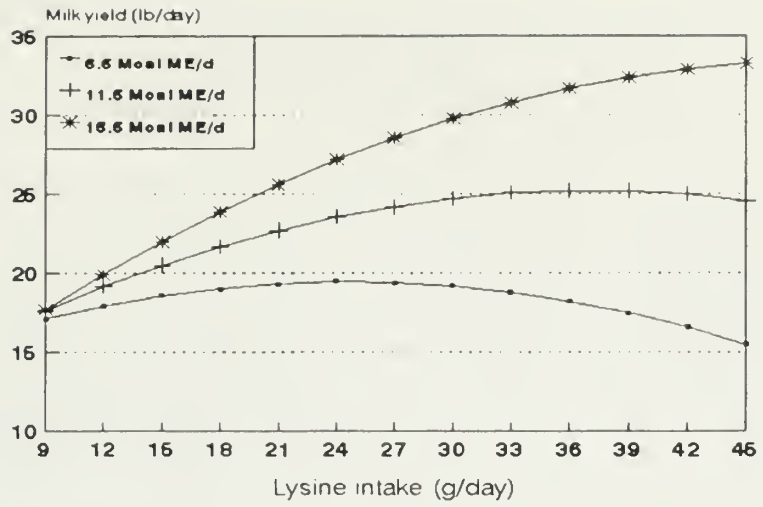

Figure 2. Predicted influence of lysine and energy intake on milk yield on day 22 of lactation (Tokach et al., 1992).

Energy. Energy is the most difficult dietary essential to supply in the diet of lactating sows in adequate amounts. In most cases, lactating sows do not consume enough feed to supply their daily energy needs. Lactating sows possess a tremendous drive to produce milk and will cannabalize maternal body tissues to satisfy the energy demands of lactation. As daily energy intake increases, loss of body weight declines during lactation and this shortens the interval to first postweaning estrus (Nelssen et al., 1985; Johnston et al., 1989). The challenge for swine producers is to maximize energy intake during lactation. Maximization of energy intake can be achieved by increasing the energy density of the diet and(or) increasing the total quantity of feed consumed.

The most common method of increasing the energy density of the diet is to add fat. Pettigrew and Moser (1991) summarized over 20 experiments reported in the scientific literature in which fat was supplemented to sow diets (Table 1). They found that fat supplementation of sow diets consistently decreased voluntary feed intake but increased daily energy intake. This increased energy intake reduced loss of body weight and supported heavier litter weaning weights. Fat supplementation of sow diets increases fat content of milk resulting in elevated energy density of milk. This elevation in energy density of milk may be responsible for the heavier litter weights observed with fat supplemented sow diets.

Table 1. Summary of responses to supplemental fat in sow diets[a]

Trait	Number of Responses		Avg. Response
	Positive	Negative	
Lactation feed intake, kg/d	3	16	-.189[b]
ME intake, Mcal/d	19	0	1.24[b]
Lactation weight change, kg	11	4	1.5[c]
Weaning to estrus interval, d	2	4	-.56
Litter weaning weight, kg	18	6	1.65[d]

[a]Pettigrew and Moser, 1991
[b]$P < .001$
[c]$P < .05$
[d]$P < .01$

Another method of increasing energy intake is to increase feed intake. Researchers have wondered how the sow would respond if feed intake and thus energy intake could be increased above the amount she would consume on a voluntary basis. Matzat et al. (1990) fed multiparous sows at 120% of ad libitum feed intake through a cannula placed in the sow's stomach during lactation (superalimentation). They reported that superalimented sows gained body weight and backfat depth and increased milk yield from 7.8 to 8.6 kilograms per day. These increases in milk yield supported increased litter weight gains from 1,590 grams per day for control litters to 2,078 grams per day for litters nursing superalimented sows. These data suggest that the "extra" energy consumed as a result of increased energy intake will not be funneled entirely into milk production. Some of the energy consumed goes to body stores which may improve rebreeding performance. Rebreeding performance and milk production probably have different economic values. At some point, our sow nutrition schemes will become refined enough to determine the marginal economic value of each additional unit of energy intake.

Historically, nutritionists have discussed energy nutrition in terms of the total calories of energy required for a given biological function with little regard for the source of those calories. Researchers in Mexico demonstrated that a diet containing 50% cane molasses, a readily available source of carbohydrates, fed during the postweaning period increased circulating insulin levels in sows and resulted in a larger litter size at the next farrowing compared with sows fed an isocaloric diet containing added fat (Rodriquez-Marquez and Cuaron, 1990). Other basic research suggests that a diet high in starch elicits higher insulin levels in blood and greater activity of luteinizing hormone in sows compared with a diet of similar energy density but supplemented with fat (Kemp et al., 1995). Luteinizing hormone plays a key role in initiating occurrence of postweaning estrus. While these basic research studies suggest that composition of the diet can have a direct influence on metabolism of the sow, recent experiments at our research farms have not been able to demonstrate similar responses when including cane molasses in the diet (Johnston et al., 1994) or when substituting starch for fat in isocaloric diets (Lorschy et

al., 1996). Our initial attempts were unsuccessful; however, further studies will likely increase our knowledge of the link between diet, metabolism, and reproductive functions so that nutritionists can include certain ingredients in the lactating sow's diet for their direct effects on body metabolism as well as for their nutrient contribution to the diet.

Until nutritionists and swine producers have a more thorough understanding of any specific metabolic effects of particular ingredients, feedstuffs will be included in lactating sow diets based primarily on their nutrient content. Energy content of a feedstuff is an important consideration. Energy dense feedstuffs are favored over lower energy feedstuffs because of the importance of maximizing energy intake. The energy evaluation system used can influence the energy value that is assigned to a particular feedstuff and hence its suitability for use in lactating sow diets. For example, wheat midds contains 3,000 kilocalories of ME per kilogram which is about 39% of the ME present in lard. Under a net energy evaluation system, wheat midds contains 1390 kilocalories of NE which is about 27% of the NE in lard (Ewan, 1991). One may place a higher nutritional value on wheat midds under a metabolizable energy evaluation system compared with a net energy evaluation system.

Protein. Dietary amino acids supplied in the form of natural proteins are necessary to maintain the sow's body, produce milk, and support growth of maternal body tissues. The first two needs are essential in the lactating sow. Fulfillment of the third need usually is deferred until gestation when the nutritional needs are not so demanding. Milk production consumes the lion's share of the total amino acids needed by the lactating sow. The amino acid needs are proportional to the level of milk production. While the sow requires 10 essential amino acids in the diet, lysine is most often first limiting in corn-soybean meal based diets. Consequently, much attention is paid to the lysine requirements of the lactating sow. Estimates of the lysine requirements of lactating sows fill the scientific literature and range from 19 to 54 grams per day (Pettigrew, 1993). This wide range of estimated lysine requirements can be explained by differences in milk production (Figure 3).

Lysine intake during lactation may also influence subsequent reproductive performance. Increasing lysine concentration of the lactation diet from .62 to 1.51% for primiparous sows had positive effects on litter growth rate (Table 3). More importantly from an economic perspective, increasing lysine concentration of the lactation diet increased size of the subsequent litter (Campbell, 1995). These data suggest that feeding during lactation sets the stage for sow performance almost four months into the future. Future research will determine if this response is repeatable in primiparous sows and occurs in older sows.

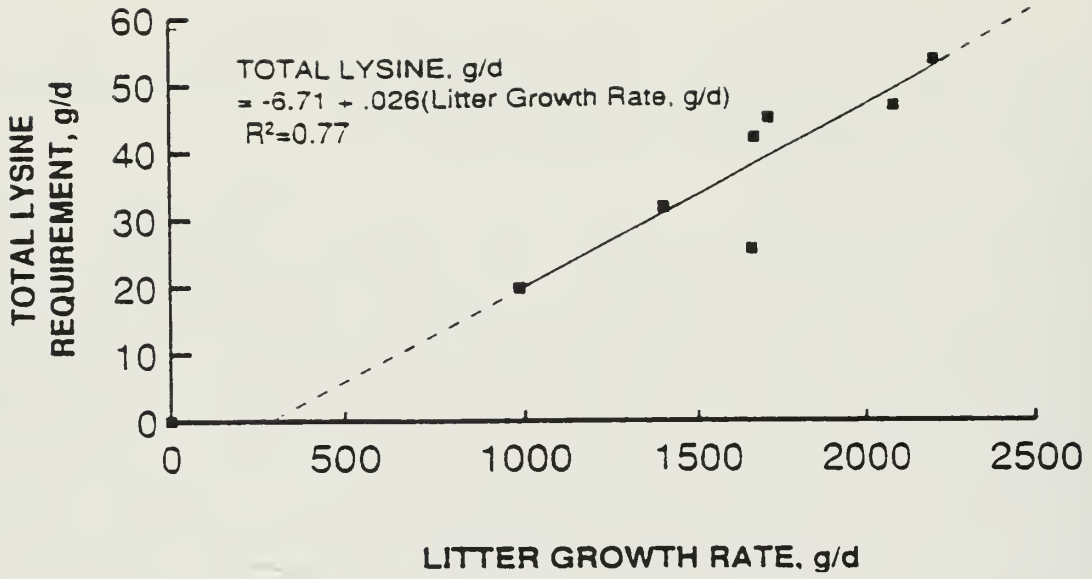

Figure 3. Estimation of total lysine requirement of lactating sows in relation to litter growth rate (Pettigrew, 1993).

Table 2. Effects of dietary lysine on performance of lactating gilts[a]

	Dietary lysine (%)				
Trait	.62	.84	1.06	1.31	1.51
Feed intake, kg/d	4.53	4.45	4.17	4.61	4.53
Lysine intake, g/d	28	37	44	60	68
Weight loss, kg	26.6	26.2	25.9	23.7	22.0
Backfat loss, mm	2.5	3.6	4.5	4.2	4.0
Pigs weaned/litter	9.0	9.4	9.5	9.4	9.8
Piglet growth rate, g/d	185[d]	212[c]	206[c]	232[b]	210[c]
Pigs born next litter	10.3	9.8	10.4	11.6	11.1

[a]Campbell, 1995
[bcd]Denotes significant differences among treatment means.

Simply stated, proteins are long chains of amino acids. The amino acids are joined in a very specific order that creates a set ratio of amino acids and this ratio is determined by the animal's genetic code. An ideal protein is one that supplies all the essential amino acids to the sow with no deficiencies or excesses. Determination of the ideal protein for sows is very difficult because she has amino acid needs for maintenance of body tissue (muscle, bone, skin, mammary gland, etc.), body growth, and milk production. Milk protein represents a large portion of the protein manufactured by a lactating sow so the amino acid pattern of sow's milk has been used by researchers to approximate the ideal amino acid pattern required by lactating sows. This approach is imperfect but still represents an advance in our understanding of amino acid nutrition of sows.

Amino acid balance becomes an especially important issue when diets for lactating sows contain crystalline amino acids. Amino acid specifications of diets can be satisfied with protein from natural sources or a combination of natural proteins and crystalline amino acids. Increasing the lysine concentration of a diet with natural proteins will also increase dietary concentrations of other essential amino acids. Generally, the desirable amino acid pattern is maintained. However, use of crystalline lysine will achieve the same objective of increasing final diet lysine concentration but concentration of other essential amino acids is not increased. This alters the amino acid balance of the diet which may or may not have negative effects on sow performance.

Recent research has suggested that high lysine diets for lactating sows that contain crystalline lysine may be deficit in valine, an essential amino acid (Tokach et al., 1993). Corn-soybean meal diets containing .9% lysine and either .75% valine (83% of lysine) or .9% valine (100% of lysine) were fed to lactating sows. Litter size at weaning was not influenced by diet but a 3.2 kilograms advantage in litter weight at weaning was observed for sows that consumed the diet containing .9% valine. The advantage in litter weight was greater in litters that contained greater than 10 pigs. These data suggest that dietary valine should be set at 100% of the lysine concentration. A subsequent study (Richert et al., 1996) conducted at the University of Minnesota in cooperation with researchers at Kansas State University revealed a significant linear increase in litter weight gain as dietary valine concentration increased from .75 to 1.15% in diets that contained .9% lysine. Results of this study suggest that dietary valine should be 117% of lysine to maximize lactation performance of sows.

Presently, the mechanism and repeatability of this valine response is unclear. If the sow truly does require valine at greater than 100% of dietary lysine, it is unclear for what functions the added valine is needed. Measurements of blood flow into and out of the mammary gland of lactating sows suggest that valine uptake represents 88% of the lysine uptake (Trottier and Easter, 1995). Valine concentration in sow's milk is about 73% of the lysine concentration (Pettigrew, 1993).

The discussion above focuses on the biological implications of dietary valine concentration on sow performance. However, one must consider the economic implications of these data. If future studies substantiate the observation that diets for high producing, lactating sows should contain valine at greater than 100% of the lysine concentration, then one must weigh the value of an additional kilogram of litter weight against the cost of supplying high valine levels in the diet. Synthetic lysine is often used to economically achieve high lysine concentrations in diets for highly productive sows. Dietary valine may be limiting in these diets. This potential valine limitation can be corrected by: 1. removing synthetic lysine and using more soybean meal; 2. supplementing the diet with crystalline valine which presently is not commercially available at a reasonable cost; or 3. including a "valine-rich" protein source in the diet. The added diet costs for each of these solutions must be less than the value of the additional litter weight gain before the swine industry will implement this concept. Future experiments will address the biological issues and determine the proper level of

dietary valine for high producing lactating sows. With more complete knowledge of the sow's valine needs, the swine industry will determine the most profitable way to apply that knowledge.

Young sows (first and second parity) seem particularly sensitive to inadequate amino acid nutrition during lactation. Presumably, this is due to the fact that these females are relatively immature with limited body tissue reserves and have a biological drive to continue growing toward their mature body weight. King (1987) argued that protein intake during lactation seemed to have a greater effect on the postweaning interval to estrus than did energy intake. In a more recent study, increasing lysine intake during lactation from 50 to 66 grams per day had little influence on litter performance but significantly reduced the weaning to estrus interval (Wilson et al., 1996). These observations suggest that young sows may deserve special attention in the form of a specially formulated diet or a topdress for the existing diet to ensure prompt return to postweaning estrus which will help keep that young sow in the herd.

New Issues to Consider with Modern Production Systems

Health status of sows. People who care for animals have known for a long time that sick animals exhibit depressed feed intake and poor performance. These same observations are true for lactating sows. Matzat (1989) observed that sows with rectal temperatures greater than 104 °F on day 1 of lactation displayed depressed voluntary feed consumption compared to sows with lower rectal temperatures. More importantly, feed intake of these sows did not return to normal levels until day 7 of lactation. These findings indicate that infections and sickness around the time of farrowing can have significant negative impacts on nutrient intake of lactating sows. This may be of particular importance in production systems that employ very short lactation lengths.

It is no surprise that clinically sick sows would not perform to expected levels. However, the effects of subclinical disease may be more obscure. Researchers at Iowa State University studied the effects of chronic stimulation of the immune system on performance of lactating sows (Sauber and Stahly, 1995). Genetically similar gilts were raised, mated, gestated and farrowed in a high health system for this study. After farrowing, half of the sows were injected with a non-pathogenic stimulator of the immune system to simulate the effects of subclinical disease. Loss of body weight and backfat during lactation, and litter size at weaning were not different between sows that did or did not receive immune system stimulation. However, voluntary feed intake, litter weight gain, and estimated yield of milk energy was depressed as a result of immune system stimulation (Table 3). From this study, one may speculate that even low level disease loads will negatively impact sow performance. This observation supports the notion that high health production systems allow pigs to express a greater proportion of their genetic potential compared with conventional production systems with a lower health status.

Table 3. Effect of immune system stimulation on performance of lactating sows[a]

Trait	Immune system stimulation		Sign. level
	No	Yes	
Sow feed intake, kg/d	5.36	4.82	.17
Sow wt. loss, kg	11.8	11.0	.83
Sow backfat loss, mm	3.0	3.8	.14
Litter size weaned	12.6	12.6	1.0
Litter wt. gain, kg	41.6	36.5	.01
Est. milk energy, Mcal/d	14.36	12.74	.01

[a]Sauber and Stahly, 1995

Leaner genetics. The continued drive to raise pigs with high lean growth potential and to produce a leaner market hog has predictably generated relatively lean sows at the time of farrowing compared with 10 years ago. On a metabolic body weight basis, the lactational capacity of lean sows is similar to that of fatter sows (Sauber et al., 1994). However, these leaner sows have less energy reserves in fat tissue that can be mobilized in support of lactation which elevates the importance of diet as a source of energy. As the industry continues to employ leaner genetics, it will become increasingly important to focus on factors that can maximize the voluntary feed intake of lactating sows.

Short lactations in Segregated Early Weaning systems. Modern, high health production systems often employ a segregated early weaning (SEW) approach to pig production. Inherent in this system is the use of short (14 to 18 day) lactation periods. Feed intake and the resulting nutrient balance of the sow is just as important in SEW systems as it is in more conventional weaning systems that use longer lactation periods. It appears that nutrient balance in the first 14 days of lactation plays an important role in determining how rapidly a sow will return to estrus after weaning. Research conducted at the University of Minnesota indicates that restriction of dietary energy during any week of a 3-week lactation prolongs the weaning to estrus interval (Koketsu et al., 1996). The goal for short lactations should be the same as for longer lactations, maximize voluntary feed intake.

Methods to Determine Dietary Nutrient Density

The appropriate nutrient density of diets is not the same for all sows during lactation. Consequently, one cannot make blanket recommendations for the energy and protein density of lactation diets and expect those recommendations to satisfy the sow's nutrient needs. Formulation of diets is farm-specific and depends quite heavily on the genetic potential of the sow and her voluntary feed intake. The **first step** in determining the appropriate nutrient density is to determine the current level of feed intake during gestation and lactation. This process will reveal if feed intake is inadequate, provide a baseline of intake against which future intakes can be evaluated, and provide nutritionists with information necessary to accurately formulaate sow diets for a specific herd.

The **second step** is to establish nutrient intake goals based on current level of milk production. The most practical method of assessing sow milk production is to measure average daily weight gain of the litter. Using average daily litter weight gain and sow body weight, compare nutrient intake levels for sows with target nutrient intakes given in Table 4 For example, a 180-kilogram sow with a litter gaining 1.8 kilograms per day has a target daily intake of 19.36 megacalories of ME and 46 grams of lysine. The nutrient intakes listed in Table 4 crudely attempt to account for lysine and protein derived from breakdown of body tissue. We assumed that sows mobilize 4 grams of lysine and 61 grams of protein daily from body tissue during lactation. The energy liberated from mobilization of body tissue is not considered. Consequently, the estimates of daily energy needs assume zero weight loss and may seem higher than is required for commercial production. The values listed in Table 4 should be viewed as intake goals rather than strict requirements.

The **third step** is to make appropriate management adjustments to maximize nutrient intake during lactation. The **fourth step** is to determine dietary nutrient concentrations so that daily nutrient intake targets can be achieved with the observed level of feed intakes. Actual nutrient intakes should match target intakes fairly closely if steps one through four were completed successfully. Improper nutrition that does not support optimal milk production during step two when litter gain is being assessed will cause an error in selecting the appropriate level of sow performance on which diet formulations are based. To be sure sows are expressing their full genetic potential for milk production and reproductive performance, producers should challenge their sows with higher daily nutrient intake to determine if sows respond with higher levels of milk production. In addition, other economically important reproductive traits such as rebreeding interval, subsequent litter size, and culling rates must be considered when determining the optimal nutrient density of diets for lactating sows.

Summary

Feeding highly productive sows is a challenging endeavor. Producers and nutritionists should consider the interrelationship among phases of the reproductive cycle when designing a sow feeding program. A better understanding of the interaction among diet, metabolism of nutrients, and reproductive functions will allow us to design more effective feeding programs that improve sow performance. The stepwise procedure presented above will allow sow feeding programs to be tailored to the conditions encountered on individual farms.

Table 4. Recommended energy, protein, total lysine, and digestible lysine intake for lactating sows by level of production[a]

	Sow Body Weight, kg											
	135				180				225			
Litter gain (kg/d)	Energy (Mcal ME/d)	Protein (g/d)	Lysine (g/d)	Dig. lysine[b] (g/d)	Energy (Mcal ME/d)	Protein (g/d)	Lysine (g/d)	Dig. lysine[b] (g/d)	Energy (Mcal ME/d)	Protein (g/d)	Lysine (g/d)	Dig. lysine[b] (g/d)
1.40	14.82	592	33	27	15.88	621	34	28	16.87	648	34	28
1.60	16.56	681	39	32	17.62	710	40	33	18.61	737	40	33
1.80	18.30	770	45	37	19.36	799	46	38	20.35	826	46	38
2.05	20.04	860	51	42	21.10	889	52	43	22.09	916	52	43
2.25	21.78	949	57	47	22.84	978	57	47	23.83	1005	58	47
2.50	23.52	1038	63	52	24.58	1067	63	52	25.57	1094	64	52
2.70	25.25	1127	69	57	26.31	1156	69	57	27.30	1183	70	57

[a] Adapted from Pettigrew, 1993

[b] Assumes 82% apparent ileal digestibility of total lysine

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Effects of Environmental Design on the Pig's Voluntary Feed Intake

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The Challenge: Inducing a Pig to Eat an Additional Few Mouthsful

Growth of the pig — without which, after all, pork production would not exist — is a process that depends on and is regulated by numerous factors. A primary biological goal in pork production is to support the growing pig so it can fulfill its potential for lean growth. Relationships among genetic potential for protein deposition; secretion rates and plasma concentrations of certain hormones; nutrient requirements for maintenance; nutrients consumed and their metabolic partition; and voluntary feed intake offer manipulatable aspects of growth, both quantitative and qualitative (Reeds *et al.*, 1993). The focus of this paper will be ***voluntary feed intake*** (***VFI***), defined as the weight of feed ingested during a given period of free access to feed (after Forbes, 1995), as related to growth of the pig.

Unfulfilled growth potential. Most pigs do not fulfill their genetic potential for protein deposition. Why not? Two important limiting factors are inadequate secretion of certain hormones and inadequate ***VFI***. A pig's ability to catalyze peptide chain elongation in muscle growth, the rate-limiting factor in lean growth, is itself ultimately limited by the pig's ability to increase ribosome number (Pain, 1986). Most pigs would be able to deposit protein in the body at a 30- to 50-percent higher-than-usual rate that could be driven by higher endogenous secretion rates or exogenous administration of certain hormones (Etherton *et al.*, 1987; Beermann, 1993; Reeds *et al.*, 1993). Moreover, although nowadays they typically ingest feed at a daily rate amounting to 300 percent to 350 percent of the thermoneutral maintenance rate, pigs which are not fulfilling their lean growth potential — whether it be determined (a) by genetically driven endogenous secretion or (b) by exogenous administration of certain hormones — would grow lean mass faster if they ingested even more feed every day (Reeds *et al.*, 1993).

This leads to another question: Can a pig digest, absorb, metabolize, and assimilate nutrients at a rate faster than that driven by normal voluntary feed intake? In an elegant experiment, Jerome Pekas (1985) surgically modified pigs so they could be superalimented. Each day for 3 weeks, a pig's digestive tract was administered 120 percent of the voluntary feed intake of its control counterpart. The result was a 13.5-percent increase in carcass growth rate over the experimental period, and the composition of the growth approximated that expected for the pertinent carcass-weight interval. In particular, the ratio of lean growth to fat growth was consistent with established norms. The pigs simply grew faster. This indicates that pigs are able to process and assimilate nutrients at a rate at least 20-percent higher than that supplied by voluntary feed intake without affecting feed-conversion efficiency or carcass composition.

Incidentally, along the line of a pig's nutrient-processing and -metabolizing limits, when a very low effective microenvironmental temperature calls for large mammals to invoke a major increase in heat-production rate in order to establish thermal equilibrium with the surroundings, they typically can sustain a metabolic rate around 500 percent that associated with the thermoneutral maintenance feed-intake rate. If the environment becomes even colder, the animal's ability to coordinate and regulate its various activities, functions, and processes begins to disintegrate, and unless this is ameliorated death soon ensues.

This paper's theme. The question comprising the theme of this paper is this:

> **If VFI is limiting a pig's lean-growth rate, how might the environment be designed so the pig would be motivated to take in a few additional mouthsful of feed every day?**

Genetic influences on *VFI*. The genetic make-up of the pigs traditionally gets a lot of attention from pork producers. Heredity does partly determine an individual pig's ***VFI***, and there is potential for genetic progress in ***VFI***. Pigs in certain genetic strains grow much faster than do those in others. And within strains, ***VFI*** is moderately to highly heritable, the estimates of heritabilty varying from .30 to .45 (Webb, 1989; Mrode and Kennedy, 1993). Moreover, ***VFI*** is correlated with growth rate (positively) and lean composition of growth (negatively), but not with feed-conversion efficiency (gain:feed ratio) (Forbes, 1995). Indeed, pigs of some genetic strains in which there has been heavy selection pressure for lean growth in an *ad-libitum* feeding situation have simultaneously experienced reductions in voluntary feed intake and growth rate (Ellis *et al.*, 1979; Laswai *et al.*, 1991).

Environmental influences on *VFI*. In addition to hereditary factors, several environmental factors also influence a pig's ***VFI*** (Forbes, 1995). Heritability estimates in the .30 to .45 range indicate that as much as 50 percent or more of the variation in ***VFI*** by pigs is due to environment and interaction between environment and genotype. Environmental factors that influence a pig's ***space*** and ***place*** are the most important in this respect. Pigs are extremely plastic, adaptable creatures (Hale, 1969; Budiansky, 1992), but even pigs have limits to their adaptability, and practical environments can be so poor as to not fall within these limits. Especially in the case of behaviors that are internally motivated (*i. e.*, emerge without direct external stimulation), if the living environment does not accommodate a particular behavior, then the pig often will be frustrated (and thereby stressed) and often will engage in a redirected behavior, *e. g.*, tail-biting (which often will be anomalous and counterproductive). Of course, the particular complement of environmental factors that together act to either constrain or stimulate feed intake by a pig varies greatly from place to place and from time to time. Hence, devising practical ways and means of designing the environment so as to motivate a pig to ingest an additional few mouthsful of feed every day is not a simple matter (Le Magnen, 1985; Toates, 1986; Taylor, 1995), especially when ***VFI*** already stands at a rate exceeding 300 percent of thermoneutral maintenance.

Some of what is known about negative environmental influences on ***VFI*** by pigs has to do with the well-known feed-intake-lowering effects of high effective microenvironmental temperature that occur as the homeothermic pigs attempt to establish thermal equilibrium with their environment (National Research Council, 1981; Curtis, 1983). The focus of the remainder of this paper, however, will be on direct effects of the social environment and direct and indirect effects of physical-environmental factors other than the effective-temperature complex.

"A Day in the Life of a Pig"

In the 1960s and 25 years later. "A Day in the Life of a Pig" was the provocative title North Dakota animal scientists gave their report (Haugse *et al.*, 1965). They directly observed around-the-clock pigs in groups of 10 that had access to both a pen in a traditional Midwestern hog barn and an outside pen. What they learned about how those pigs spent their days might have surprised some people. During warm weather, the pigs spent roughly 79 percent of the time (19.0 hours daily) resting (lying or sitting); 13 percent (3.1 hours) eating; and only 8 percent (1.9 hours) engaged in all other activities (*e. g.*, defecating, drinking, urinating, walking, playing, and interacting socially with groupmates). The pigs moved from one place or resource to the next, but "spent very little time [simply] walking about". They averaged 32 "trips to the feeder" each day, and spent a total of 136 minutes daily eating, so each meal lasted approximately 4.3 minutes.

Today's pigs in groups of 16 residing in a conventional naturally ventilated intensive growing-finishing house with partly slotted concrete floors here at the University of Illinois followed very nearly the same schedule (Pedersen *et al.*. 1997): 83 percent (19.9 hours daily) lying or sitting; 9 percent (2.2 hours) eating; and 8 percent (1.9 hours) engaged in other activities. These pigs spent 6 percent of each day (1.4 hours of the 1.9 "other" hours) moving (walking or running), again mostly from one place or resource to the next. They averaged 26 meals daily, and spent a total of 132 minutes daily eating, so each meal lasted approximately 5.1 minutes.

Strikingly similar. Despite the inevitable genetic and environmental differences across those 25 years, the similarity between the pigs' activity budgets is striking. This suggests that pigs' daily activities are highly structured. The minor discrepancies between the two experiments — *viz.*, the 0.9-hour trade-off between eating time and resting time and the differences in number of meals daily and meal length — plausibly owes to the better design of the feeding places at Illinois, which the pigs might have found more accessible and more private, as will be discussed later. In any case, we may conclude that pigs spend 4 to 5 hours daily engaged in activities involving social interaction of one sort or another. Over half of this time seems to be directly related to eating, and therefore to ***VFI***.

Digression for Definitions

After J. M. Forbes (1995), distinct eating periods which may include short breaks but which are separated by longer intervals are called ***meals*** and the short within-meal periods of eating are called ***eating bouts***. In analyzing eating behavior, a minimum ***intermeal interval*** often is calculated from a frequency plot of noneating intervals, meals separated by intervals of less than this value being considered as part of the same continuing meal. The ***hunger ratio*** is calculated as weight of meal divided by premeal interval, ***satiety ratio*** as weight of meal divided by postmeal interval. Feed ingested per unit time in a given meal is called ***eating rate***, mean eating rate for a day ***intake rate***. The total weight of feed ingested in a given period of free access to feed (usually a day) is called ***voluntary feed intake***, which usually is less than the ***potential feed intake*** (the weight of feed required to fulfill all of the animal's nutrient requirements) due to either internal biochemical or physical constraints, environmental limitations, or both.

Social Environment, *VFI*, and Growth in Pigs

Social environment. Those aspects of a pig's microenvironment that result from the presence of other animals comprise the pig's ***social environment***, which varies in time and the nature of which is determined by numerous animal, chemical, physical, and other biological environmental factors. Domestic pigs possess all of the behavior patterns their wild progenitors do, although for some behaviors stimulus thresholds and response magnitudes have become modified as the domestication process has taken place (Price, 1968; Stricklin and Gonyou, 1995).

For one thing, domestic pigs continue to be ***opportunistic omnivorous scavengers***, and as such they recognize the need to cooperate with others of their kind, hence they do not establish and protect territories as many other species do. Yet they seem to be extremely aware of themselves and hence ***selfish***, resulting in competition for access to vital resources (*e. g.*, feed, water, mates, resting and wallowing areas). Pigs reconcile the inevitable conflict between cooperation and selfishness — thereby circumventing perpetual fighting over control of a resource — by establishing and maintaining, in teleologically advantageous fashion, ***social order***: they establish ***social hierarchies*** (otherwise called ***dominance hierarchies***, ***dominance orders***, or ***rank orders***).

Social hierarchies. Through their self-impressions, pigs are aware of their own individual capabilities, and they are aware of the relative capabilities of their groupmates, as well. Either acute, temporary fear of a groupmate or chronic shyness is associated with a relatively low self-impression, and an animal possessing such an emotion will tend to rank lower in the social hierarchy than if it is more confident of its relative prowess. These impressions of itself and of groupmates that a pig possesses result from ***dyadic agonistic encounters*** between every pair of pigs in a group. Of course, as group size increases arithmetically, the number of dyadic encounters required to establish the social hierarchy increases geometrically. These rank-determining skirmishes range in intensity from simple threat displays all the way to life-and-death struggles, and usually occur within the first day or so after a new group has been formed. Body weight (heavier pigs tend to dominate), gender (males and castrates tend to dominate), and strength of motivation to succeed in fighting seem to be the major determinants of the outcomes of a round of aggressive bouts.

As will be discussed again later, pigs are relatively feisty creatures, and so their social hierarchies are relatively unstable. Especially among pigs ranking in the middle of a hierarchy there may be little difference in ability to dominate, and this tends to lead to revolts against the established social order, involving challenges to higher-ranking pigs by lower-ranking pigs. In any case, ***social stability*** depends on each pig being able (a) to recognize every other pig in the group when their paths cross in their normal daily activities and (b) to recall its own hierarchical rank relative to that of every other pig. Pigs recognize one another by means of smell, of sound, and somewhat by means of sight (Ewbank *et al.*, 1974). Of course, as group size increases, the number of individual pigs to be remembered — *i. e.*, recognized and categorized — increases, whereas the frequency of chance encounters tends to decrease. There is, consequently, a tendency for group social stability to wane as group size increases.

Another factor that contributes to ***social instability*** is poor environmental design. When pigs, in effect, are forced by either inadequate space or inadequate place to compete for vital resources, conventional social hierarchies will break down, and their advantages will be lost.

Social rank and growth. A pig's social environment affects the nature of its growth (Gonyou, 1993). Glenorchy McBride and colleagues characterized influences of an individual pig's rank in the social hierarchy on its growth. Birth weight and teat order were found to be primary determinants of 3-week weight (McBride *et al.*, 1965). In turn, 3-week weight determined social rank in postweaning groups, and body weight of individual pigs at 8, 12, and 16 weeks of age, respectively, was determined primarily by weight at the previous weighing and by social rank (McBride *et al.*, 1964). In particular, at both 8 and 16 weeks of age, social rank accounted for approximately 15 percent of the variation in body weight. A similar relationship was found by Beilharz and Cox (1967). Assessing this relationship between social rank and growth may be an effective way of identifying a production system having deficient design, but probably would be of limited usefulness in determining whether the system provides an appropriate amount of total space per individual (Stricklin and Gonyou, 1995).

Negative effects of social interaction. Pigs have notoriously unstable dominance orders, with revolts and challenges to the established social hierarchy being more common in this species than in others. Also, pigs are relatively feisty as they engage in severe competition for various environmental resources, *e. g.*, place at feeder, place at waterer (especially during hot weather), place for resting (Wood-Gush, 1990).

McBride (1968) suggested that an individual animal's performance depends on (a) its social rank and (b) its access to critical resources. When access to resources is unlimited, all individuals should be expected to perform near their respective potential levels. However, when access is limited — as often happens in agricultural settings — only the high-ranking individuals should be expected to achieve their performance potentials.

Most affected: smaller pigs or middleweight pigs? Putative evidence supporting this notion includes results with growing pigs showing that, when access to place at feeder was abundant, there was no correlation between social rank and growth rate, but when feeder space was markedly limited, pigs in the upper half of the social hierarchy outgained those in the lower half by 14 percent (Hansen *et al.*, 1982). The conventional theory for the cause of this effect has focused on access to place at feeder and consequently ***VFI***. It also has been observed, however, that low-ranking pigs may be forced to rest in locations in the pen which provide relatively undesirable microenvironments (Ewbank, 1969).

In a creative approach to studying this phenomenon, Aaron Moore and Harold Gonyou measured rate of body-weight gain in pigs while they were in the lighter half of the group through when, via systematic regrouping, the same pigs were in the heaviest quarter of the group. When they were light relative to groupmates, their growth rate was low; when they were relatively heavy, their growth rate was high, even surpassing that of their counterparts in single-age, uniform-weight groups (Moore, 1990; Gonyou, 1993).

Other evidence, however, indicates that it is growth of the middle-ranking pigs in a group that is most negatively affected by social pressure. There generally exists a positive relationship between body weight and social dominance rank. Also, in agonistic encounters involving two pigs, the greater the difference in their body weights, the fewer, shorter, and less intense are their encounters tend to be (Rushen, 1987). Large and small pigs, respectively, grew faster in variable-weight groups (in which dominance-subordinance relationships presumably were relatively clear-cut) than in uniform-weight groups, whereas middleweight pigs grew faster in groups composed of middleweight pigs only (Gonyou *et al.*, 1986). Of course, in variable-weight groups composed of pigs of all body weights, middleweight/middle-ranking pigs must deal with both social-dominance pressure from larger/higher-ranking pigs as well as social-challenge pressure from smaller/lower-ranking pigs.

Despite remaining unknowns, the social environment clearly seems to markedly affect pig performance.

Group Size May Affect *VFI* and Growth Rate

There is ample evidence that social tension reduces ***VFI*** by pigs (Patterson, 1985; Spicer and Aherne, 1987; Gonyou *et al.*, 1992). In the Illinois work, pigs in groups of five ate ~5 percent less feed and grew at only 96 percent the rate of individually penned counterparts (Gonyou *et al.*, 1992). Pigs in groups of 5, 10, or 15 were observed actively avoiding one another in the vicinity of the feeder, and individuals in group pens spent more time standing — as they do when waiting for access to place to feed — than did those in individual pens (Gonyou,. 1993).

It is generally accepted that group size *per se* and rate of body-weight gain are inversely correlated (Kornegay and Notter, 1984), although conclusions must be cautiously made because either experimental or empirical observations along this line may be biased by artifacts of confounding due to (a) interaction between group size and space allowance and (b) inadequate environmental design resulting in reduced ***VFI***. Nevertheless, such a relationship may hold over some range in group size — say, 5 to 50 pigs in a pen. Indeed, for reasons still unknown, social instability appears to be most obvious when group size is on the order of 30 to 50 pigs in a pen. Casual observations on pigs in larger and even very large groups — say, on the order of 50 to 500 pigs in the same pen, *and provided there exists adequate access to important environmental resources* — indicate that the animals establish numerous smaller social subgroups (often numbering around 25 pigs each) and perform as well as would pigs in a pen group of 25 (McGlone, 1996).

Social Dynamics and Growth Setbacks

Regrouping pigs. In pork production, pigs may be regrouped several times between weaning time and marketing time in attempts to economize in the use of facilities. Harold Gonyou (1993) called this practice the ***"some in, some out"*** approach. Of course, a group of pigs does not appreciate intruders, whether the latter moved in of their own volition or not, and the intruders are always the object of a series of fights with at least the higher-ranking pigs already part of the group. Moreover, either adding pigs to or taking them from an established social group provokes a new round of ***dyadic agonistic encounters*** between *all* of the individuals in *all* of the new groups as the pigs intently set about updating social hierarchies.

As expected, especially when access to resources is marginal, regrouping leads to less aggressive behavior in pigs in variable-weight groups than in uniform-weight groups (Tindsley and Lean, 1984; Moore, 1990; Gonyou, 1993).

The intense, one-on-one aggressive encounters typical of dominance-order establishment may cause injury and even a *temporary* setback in rate of body-weight gain, presumably because of reduced feed intake, increased energy expenditure due to fighting activity, or both. Nevertheless — provided the environment affords the pigs adequate access to resources — the long-term consequences of regrouping may be nil (Sherritt *et al.*, 1974).

Realistically, the fact that the adequacy of agricultural environments in this respect varies among facilities is a cause for concern with respect to both the pigs' productivity and their state-of-being.

- When multiple stressors act simultaneously or sequentially, their respective effects are both additive and interactive (Baxter, 1984; McFarlane *et al.*, 1988; Johnson *et al.*, 1991). Thus, when additional stressors — *e. g.*, frustration due to inadequate place at feeder (Sherritt *et al.*, 1974) or high environmental temperature (McGlone *et al.*, 1987) — coincide with regrouping of pigs, the intensity of fighting may be extreme, the growth check *permanent*..
- Both the physical injury and the psychological stress consequent to agonistic encounters negatively affect a pig's state-of-being, which is of concern with respect to the animal-welfare issue.
- When the ordinarily temporary growth setback due to regrouping occurs within, say, 2 weeks of a pig's being marketed, that individual may not have enough time to compensate, and the setback in effect becomes permanent (Stookey, 1991; Gonyou, 1993).
- Insidious inadequacies of typical pork-production systems with respect to engendering productivity-neutral social environments have precluded the use of swine of certain genotypes due to extreme susceptibility to the social stresses commonly encountered (Symoens and van den Branda, 1969; Gonyou, 1993).

Tail-biting. Tail-biting is a behavioral disease that may break out in grouped pigs residing in intensive-production facilities. It leads to significant reductions in productive performance and even death (England and Spurr, 1967; Jericho and Church, 1972). Tail-biting seems to be of multiple etiology, although its causation is not yet well understood (van Putten, 1969; Fritschen and Hogg, 1983; Fraser, 1987; Fraser *et al.*, 1991). Environments that are suboptimal in several specific ways (*e. g.*, air quality, effective temperature, inadequate access to resources, and other sources of social tension) and dietary deficiencies (*e. g.*, protein, salt, and trace minerals) continue to be suspected as primary triggers of tail-biting outbreaks. Tail-docking is the widespread practice employed to reduce the incidence and severity of tail-biting, but of course eliminating the object of this vicious behavior — the tail — does not eliminate the causes of the behavior.

Space and Place

Quantity versus quality. In a pig house, ***space*** is a major determinant of ***place*** — as in place to engage in maintenance and social behavioral activities, *e. g.*, eating, defecating, drinking, urinating, playing, socially interacting, and, perhaps, grooming. The distribution of living space and the location in it of vital resources — space and place (Baxter, 1984) — are two critical features in the sound design of animal accommodations. Because of the relentless pressure in the pork-production industry to minimize the cost of pork production, there is ever-present pressure to minimize the cost of living accommodations for pigs. A consequence of all this is inevitable pressure to minimize the size of the accommodation facilities, which tends to reduce both capital and operating costs. It should be kept in mind, however, that ***quantity of living area*** and ***quality of living space and place*** are not equivalent, and that often a given space can be improved with respect to *quality of place* by *arranging* that space more appropriately.

Functions of space. By moving, animals behave, and thereby control their environment (Stricklin and Gonyou, 1995). Each pig in a social group carries with it its own individual ***portable space***, by which it establishes ***groupmate distance*** relative to groupmates, akin to ***flight distance*** with respect to perceived predators (sometimes including humans). The quantity of portable space a pig has varies with (a) the behavior in which it is engaged and (b) its rank in the social hierarchy.

As the space allowed a group of pigs increases, the point is reached where no single pig can uniformly control all the space in the pen. Moreover, as pen size increases and also when pigs in any size of group or pen are crowded, the efficacy of interindividual threat and submission cues can break down, which tends to increase ***social tension*** and even lead to what is called ***social stress*** (McBride, 1971; Stricklin and Gonyou, 1995), both harbingers of ***social instability***.

Spacing behavior. Ray Stricklin and Harold Gonyou (1995) have suggested approaching animals' space needs in terms of their ***spacing behavior***, behavior patterns animals invoke so as to fulfill their movements and orientations associated with groupmate distance, flight distance, and maintenance behaviors (*e. g.*, ingestive and eliminative behaviors). They went on to suggest that, for animals, "area is to spacing as food is to nutrition. As food in many forms can meet the nutritional requirements of animals, with some forms more complete than others, area can be provided in many forms, some probably more complete than others in meeting the ***spatial needs*** of animals."

Space versus area. Extending the above line of reasoning regarding *quantity of space* versus *quality of space and place*, then the concepts *space* and *area* are not equivalent (Stricklin and Gonyou, 1995). Pigs use differentially a given pen area that is configured in different ways. For example:

- Rectangular pens have four corners, triangular pens three, circular pens none. Pigs use corners to escape aggressive groupmates and prefer corners as place to defecate (Wiegand *et al.*, 1994).
- When the area of a square pen is increased, *e. g.*, by a factor of 2, ***pen perimeter*** and ***pen diagonal***, respectively, increase by only a factor of $\sqrt{2}$ (*i. e.*, ~1.4). This is important because, to a pig, (a) the pen perimeter is the preferred resting place (Wiegand *et al.*, 1994) and (b) pen diagonal determines the maximum distance between two pigs.
- An equilaterally triangular pen has 28 percent more pen perimeter, and a square pen 13 percent more, than a circle pen of equal area; hence, in terms of resting area, triangular pens presumably maximize the efficiency of area use of pigs (Wiegand *et al.*, 1994).
- The more oblong a rectangle, the greater the ratio, perimeter:area, but soon (with area remaining constant) very long pens become impractically narrow (in terms of maneuvering space), although the rectangles do maximize pen diagonal distance. Pigs may organize themselves socially into several smaller subgroups in rectangular pens (Wiegand *et al.*, 1994).

Space over time. Pigs observe daily activity schedules, and these tend to be synchronized among individuals. So time also must be considered when designing pig accommodations in terms of space. Some places are so physically different as to be mutually exclusive (*e. g.*, in most systems pigs cannot eat while standing at place to drink and would prefer not to defecate where they rest or to rest where they defecate), but in other cases — provided the pigs' activity schedule permits — there can be overlap of *places* in the very same *space*.

Places Within Spaces

Seaton Baxter overall approach. Baxter (1984) suggested the following approach to designing a pig pen so as to support pig well-being, health, and performance.

- *1. Assign four places in the pen:*
  - Place to eat feed
  - Place to drink water
  - Place to eliminate feces and urine
  - Place to rest
- *2. Consider environmental features characteristic of each place, respectively:*
  - Feeder
  - Waterer
  - Slots, perforations, or holes
  - Comfortable floor
- *3. Allocate space to each place:*
  - See *"Place to eat"* (below)
  - See *"Place to drink"* (below)
  - See *"Place to eliminate"* (below)
  - See *"Place to rest"* (below)
- *4. Determine opportunities for spatial overlapping*
- *5. Integrate design features*
  - Match location of environmental features to pigs' needs and preferences

Place to eat. Place to eat is the place to start the design of a pig pen. Design of a sound *ad-libitum* feeding place is critical to supporting unimpaired ***VFI***, and the process is complicated (Baxter, 1984; Taylor, 1995). Again, remember: group size, pen size and shape, and resource locations in the pen have marked effects on ***pen dynamics***, influencing a pig's access to feed, and thus ***VFI*** (Taylor, 1995). And remember, too: Pigs prefer a private and secure place to eat; addition of a solid or partial partition between adjacent eating places at a feeder trough in effect increases the number of places to eat, provided each place is adequately designed in other respects, especially headroom.

- Using the following approach as well as other knowledge, determine number of places to eat needed
  - Knowledge of ***time-sharing of places to eat***, which differs across age/weight ranges, permits estimation of the number of pigs one place to eat can accommodate
    - Each pig spends ***A*** hours daily eating
    - Around ***B*** percent of a pig's eating time comes during the 12-hour daytime period (typically somewhat >50 percent [Pedersen, 1992])
  - So each pig spends ***C*** daytime hours eating
  - And so, *e. g.*, with ***D*** pigs in the pen:
    - Multiply ***D*** pigs by ***C*** daytime hours = total ***E*** daytime hours eating by the ***D*** pigs
    - Divide ***E*** total daytime hours eating by 12 daytime hours = ***F*** places to eat

        - Multiply the value so calculated by a factor that will account for the fact that, in view of inevitable social tension regarding access to place to eat, the feeder should not be expected to be fully occupied all the time
    - Recommendations by Dr. Ian Taylor and Dr. Jim McFarlane of Animal Environment Specialists, Inc., Columbus, Ohio (weight range/number of pigs per place to eat): pigs weighing <7 kg/2 pigs per place to eat; 7—22 kg/3; 22—45 kg/4; 45—113 kg/5
    - Remember: If the eating space provided by a feeder limits a pig's normal range of eating movements, or if the places to eat are spaced so closely together that the indicated number of pigs cannot simultaneously stand shoulder-to-shoulder and eat comfortably, then the use of such standard recommendations will not suffice to support unimpaired ***VFI*** (Taylor, 1995)
- Determine size of each place to eat (Taylor, 1995)
    - Industry norms still do not offer enough headroom at the feeder to permit a pig to freely eat, and this results in decreased ***VFI*** and increased feed wastage
    - Design deficiencies also are associated with variation in length and frequency of eating bouts and meals and with the nature of aggressive encounters at the feeder
    - Both width and height of feeder headroom are important
        - For some designs, the act of eating *per se* is difficult, uncomfortable, or both, so pigs decrease duration and increase frequency of eating bouts and meals, consequently increasing the social interaction at the feeder
        - A pig signals difficulties with eating by assuming anomalous eating stances, *e. g.*:
            - Pig tucks its head or forces contact of its snout/head with feeder or its mandible/ventral neck with the trough lip
            - Pig assumes diagonal approach into feeder, often with flip-flopping of this diagonal stance, indicating less-than-adequate front-to-back headroom
            - Pig frequently changes posture during and especially between eating bouts, often including backing away from feeder as it completes each swallow (and often dropping feed outside the feeder in the process)
    - Eating-place width recommendations by Dr. Ian Taylor and Dr. Jim McFarlane of Animal Environment Specialists, Inc., Columbus, Ohio (weight range/width of each place to eat): pigs weighing <7 kg/9 cm wide; 7—22 kg/15 cm; 22—45 kg/25 cm; 45—113 kg/35 cm
    - Floor-space at the place to eat is crucial, too
        - From empirical measurements, Baxter (1984) gave formulas for estimating static dimensions of pigs over the weight range of 2 to ~300 kg
        - All formulas are of similar form — nominal dimension = $k\ W^{.33}$ — where ***k*** is the particular coefficient for the dimension of interest (cm) and W is the pig's body weight (kg)
            - Various values for ***k*** are:

width at shoulders	6.1	length tail—snout	30.0
width at middle	6.4	height at shoulders	15.0
width at rump	5.9	height at rump	15.6
length tail—shoulders	18.5		

        - For example, a pig weighing 100 kg would be ~28 cm wide at the shoulders:
            - $W^{.33} = 4.57$; ([6.1] [4.57]) = 27.9 cm
            - Notice how this estimate compares with the AES place-to-eat width recommendation of 35 cm for pigs in the 45—113-kg range (above)
        - Similarly, a pig weighing 100 kg would be ~85 cm long from tail to shoulder, hence such a pig would require an undisturbed floor space ~28 cm wide and somewhat >85 cm long in front of the feeder (assuming its head is positioned over the feeder trough)
- Determine location of place to eat
    - Location of place to eat is fixed by feeder location
    - *Actual* access to feed and ***VFI*** are determined by feeder location as well as feeder design (integration of places in a pen is discussed below)

Place to drink. On average, the year around, a pig will take 25 to 30 drinks daily (>30 during hot periods, of course), most of them only a few seconds in duration and almost all during daytime. Because a pig that has been displaced by a groupmate from a place to eat often redirects its attention to a waterer, waterers should be located near — but not necessarily in combination with — feeders. Based on estimates along the above lines, a 100-kg pig occupies a space ~140 cm long (tail-to-snout) and ~28 cm wide while drinking from an operant waterer.

Careful, continuous attention should be paid waterer design and operation, too (McFarlane, 1995), including:

- Appropriate water-delivery rate — at least 1 liter per minute (Olsson, 1983)
- Appropriate height for comfortable access by the pigs expected to drink from it
- Appropriate pig-biology-based design in terms of movement and size
- Appropriate number of secure places to drink — always more than one waterer per pen (located an adequate distance apart from each other/one another that a dominant pig cannot at once control all places to drink) and never more than 20 pigs per waterer

Place to eliminate. A pig will defecate and urinate several times daily. Pigs tend to eliminate feces and, to a lesser extent, urine at a discrete place away from their chosen resting place, probably because they prefer the place to rest to be comfortable and to lie on feces or urine tends to lower the effective microenvironmental temperature (see below). Four times out of five, a preferred place to eliminate will also be a very secure place from a pig's point of view (see below). Unfortunately, this sometimes means that pigs will (exasperatingly) choose to defecate routinely in the feeder trough (Baxter, 1984; Taylor *et al.*, 1986; Taylor, 1995).

Pigs seem to deposit excreta in a place that is not being used *at the moment* for another purpose. Interestingly, individual pigs in a group tend to have their own respective preferred elimination places. But they observe a social hierarchy in regard to place to eliminate, too, so a low-ranking pig does not always get to defecate or urinate in its preferred place, sometimes giving the appearance, at least, that it is relatively indiscriminate in its elimination patterns (Baxter, 1984).

Place to rest. Ample comfortable, undisturbed floor space should be provided to accommodate all pigs lying simultaneously. Pigs prefer to rest away from the place to eliminate, probably because the inevitable body-surface wetting associated with lying on feces and urine in effect reduces effective microenvironmental temperature. Pigs choose a place to rest primarily on the basis of thermal comfort, and if possible will avoid chilly floor conditions or drafts.

Incidentally, because of the resting-place and elimination-place preferences of the pigs, the presence of "dirty" pens and pigs is almost always a sign of poor ventilation-system design, operation, or both. In houses equipped with ventilation systems having inadequate airflow-direction control, the comfortable part of a pen might differ at different times of the day. In such cases, the pigs may, from time to time, choose to lie all over the pen, and consequently over a 24-hour period they will eliminate all over the pen, which results in their lying in excreta most or all of the time.

The wild progenitors of domestic pigs are primarily a prey species, hence their innate preference is to choose a secure lying place for resting. In a pig pen, this means pigs usually will choose to lie with their backs to a pen partition. Such a strategy on the part of a pig also minimizes being disturbed by penmates on the move to feeder or waterer. Hence, place to rest should be associated with pen partitions.

The floor area required by groups of pigs for place to rest varies with effective microenvironmental temperature. During cool periods, the pigs' lying postures (Grommers *et al.*, 197X) and huddling with neighbors (Mount, 1968) result in less floor area being required for resting. Christopher Boon (1981) estimated that the total floor area (m^2) required as a place to rest by a group of pigs varies from .017 $W^{.67}$ to .023 $W^{.67}$, where W is the sum of body weights (kg) of pigs in the group. Hence, *e. g.*, a group of 25 pigs weighing on average 100 kg each requires a maximum (during warm periods) of ~4.35 m^2 floor area for place to rest, and pig pens should use this sort of value as a design criterion.

Total pen floor area. Baxter (1984) approached determining a pig's total pen floor area requirement from the point of view of its being the sum of the respective spaces needed, *viz.*:

- body space — the static, physical space occupied by a pig's body
- dynamic space — the extra space a pig requires as its changes posture or position in the pen
- social space — the space accounting for a pig's "groupmate distance"
- residual space — wasted space; ideally nil but realistically unavoidable

Moreover, floor area needed per pig will generally decrease as group size increases (McGlone and Newby, 1994), as the actual cumulative ***free space*** increases as group size increases.

Current recommended total pen floor area allowances per pig for pigs in groups of 5 to 20 pigs are: body weight 5—27 kg/.54 m^2; 25—57 kg/.90 m^2; 57—125 kg/1.26 m^2 (FASFAS, 1997), more than typically allowed in the pork-production industry today.

Integrate design features. Overall pen geometry is crucial. Ignoring this critical final step can lead to reduced pig access to feeder — often resulting in reducing ***VFI***, as well as ill-defined and precariously located nominal resting and eliminating areas.

For instance, a pen <2.3 m wide (outfitted, as is typical, with a multiple-place *ad-libitum* feeder located along a pen-side partition) provides inadequate clear distance between feeder trough lip and opposite pen partition, barely enough space for either (a) larger pigs (*e. g.*, ~1.4 m long at 116 kg) to stand perpendicularly to feeder while eating or (b) maneuvering space for two pigs coming from and going to feeder, often resulting in a place to eat at the end of the feeder not being used much or even being used as a place to defecate — all contributing to lowering ***VFI***. Nevertheless, use of "narrow pens" has been on the increase in the pork-production industry in association with the trend to smaller group sizes (15 to 25 pigs per group) and the consequent default determination of pen width by dividing recommended total-pen floor-area allowance by popular building widths (*i. e.*, pen lengths) (Taylor, 1995).

Again, overall "area allowance" may be adequate, but pen geometry, small group size, and social dynamics combine to hamper pig movement to and from the feeder.

- Sometimes movement to and from the feeder disrupts pigs in the resting area
- Sometimes there is little free space available for maneuvering and avoidance, which can increase social conflict and stress as well as injury to feet and legs

Finally, consideration should be given to intentionally furnishing pig pens with **place to hide**, which pigs can use to escape aggressive penmates (Nehring, 1981; McGlone and Curtis, 1985). These features probably are most useful during the process of social-hierarchy determination the first few days after new group formation. However, extremely shy pigs will use such havens even after the social group has been organized. Partitions between adjacent places to eat at the feeder trough (see above) often serve this purpose. Of course, a pig occupying a place at the feeder simply for the purpose of "hiding" from a penmate is at the same time making it impossible for any other pig to use that place to eat, so separate features may be advisable as another means of maximizing ***VFI***.

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Feed Intake Behavior and Implications for Energy Utilization

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The study of feed intake has been greatly facilitated by the recent development of computerized systems that monitor the feed intake of individual animals within a group. Such equipment was originally designed for use by breeding stock supply organizations in the performance testing of pigs in group situations. The majority of selection programs for pigs place considerable emphasis on feed efficiency because of its impact on production costs. Historically, genetic improvement in feed efficiency was achieved as a correlated genetic change resulting from selection for growth rate and carcass lean content for animals tested in groups, where individual feed intakes could not be measured. Alternatively, pigs were penned and fed individually to obtain feed intake data, a procedure that is expensive in terms of both labor and facility costs. In addition, animals that are genetically superior when penned as individuals may not perform the best in group-housed situations i.e. under commercial conditions. Studies that have compared the growth and carcass characteristics of boars that have been individually fed during the performance test with the performance of their progeny under commercial group-housed conditions. These have generally shown moderate to low correlations between performance in the two environments. This phenomenon is termed a genotype x environment interaction and suggests that different genes may be involved in controlling growth performance in group-versus individually housed animals. Thus, breeding organizations stimulated the development of feed intake recording equipment to allow them to test and select animals in a social environment similar to that experienced in commercial production.

Computerized feed intake recording systems are generally used with growing-finishing pigs and they have the capacity to take pigs between live weights of approximately 20 to 150 kg. They comprise a feed station, which consists of a single-space feed trough attached to a load cell, an antenna that picks up signals from the individual pig transponders, control equipment and a computer which collect and store all of the data on feeding activity at the feed station. The feed station generally has some form of a protective race which ensures that only one pig can access the feed trough at any time. The major difference between the various systems that are commercially available is in the design of the protective race, which vary from low to high levels of protection for the feeding pig.

When a pig enters the feed station, the signal from its ear tag transponder is picked up and the identity of the animal is recorded, together with the time of the visit and the weight of the feed trough. The same information is recorded as the animal leaves the feed station and the amount of feed consumed and the time spent in the feeder is obtained by difference. Data on feed consumption at each visit is accumulated over time to give daily and total test period feed intakes for each animal in the group.

A number of commercial designs of computerized feeders have been developed including the

following:

ACEMA - 48 (Centre d'Etudes du Machinisme Agricole, du Genie Rural et des Eaux et Forets, F-35000, Rennes, France)

Feed Intake Recording Equipment (FIRE, Hunday Electronic Ltd, Newcastle upon Tyne, England; Osborn Industries, Osborn, Kansas).

Individual Voluntary Feed Intake Recording in Group Housing (IVOG, Technical and Physical Services in Agriculture, Wageningen, Netherlands)

Tedea Modal 1250 (Tedea, Israel; Eweka Electronic Identification System, Pittsburg).

This later system is designed principally for research use with the other three systems being designed largely for use for performance testing breeding stock to obtain data on the total amount of feed consumed by individual animals. However, they also provide a considerable amount of detail on the feeding activity of animals in groups including data on the following:

- the time and duration of visits to the feeder
- the amount of feed consumed at each visit
- the feed consumption rate (which has generally been defined as feed consumed ÷ time in the feeder).

This equipment, therefore, has the potential to be a valuable research tool which can be used to provide an insight into feeding behavior. A FIRE system was installed at the University of Illinois in 1993 and the results of our studies are presented, along with research from other centers, in this paper.

An interesting feature of computerized feed intake recording equipment is that it generates a huge amount of data relative to feed intake. The results of a recent study carried out at this center involving 120 pigs over a 10 week period illustrate this point (Hyun et al., 1996). Animals visited the feeder on average 12 times per day and for each visit the time of entry and exit and the weight of the trough before and after each visit in the feeder were recorded directly. From this information, the time spent in the feeder and the amount of feed consumed at each visit are calculated, thus producing an average of over 5000 observations for each individual pig and more than 700,000 total observations for the study relating to feeder activity.

A recent development has been to addition of a weighing platform to the feed station which allows the weight of animals to be automatically recorded at the same time as their feed intake. From the standpoint of genetic improvement programs, it is now theoretically possible to select pigs that have specific growth and feed intake curves. For example, it may be possible to select animals that have higher feed intakes during the growing phase and lower feed intakes during finishing.

Despite the widespread use of this type of equipment by the seed stock industry, there is surprisingly little information on the most appropriate conditions for its use, particularly in terms of group sizes and space allocation. Manufacturers' recommendation have been to allow relatively large amounts of space per animal, up to twice the normal recommended levels for commercial pigs. However, this recommendation appears to be related more to reducing ear tag loss than to any consideration of the impact of space allocation on performance levels or feeding behavior. Early versions of the FIRE system used relatively large ear tag transponders which were subject to a high level of losses. However, more recent versions use a much smaller transponder which has much lower loss rate.

We have recently completed a study on the FIRE system investigating the influence of group size of 2, 4, 8 and 12 pigs per pen for animals between 25 kg and 50 kg live weight, at a stock density 0.9 m^2/pig (Hyun and Ellis, 1996). The results of this study are summarized in Table 1 and Figure 1. Daily feed intake and live weight gain decreased with group size, largely as a result of a reduction in the total amount of time spent in the feeder each day; pigs in groups of 12 spent approximately 24 and 29 minutes less time in the feeder and consumed 0.20 and 0.16 kg less feed per day than groups of 2 and 4 pigs respectively (Table 1). The diurnal distribution of feeder visits (Figure 1a) was characteristically higher during the daytime (0600 to 1800 h) than during the nighttime. However, feeder activity for the groups of 12 pigs showed much less diurnal variation than for the smaller groups and the percentage of time that the feeder was occupied increased with group size and approached 100% for most of the 24 h period in the largest groups (Figure 1c). Further research is in progress to investigate the impact of group size on growth and feed intake traits in finishing pigs.

The major difference between the FIRE system and conventional commercial feeders is the presence of the protective race in front of the feed hopper. Nielsen et al. (1995b) investigated the effect of three different entrance designs on growth performance and feeding behavior in groups of 10 pigs between 34 and 57 kg live weight. The designs compared were a short race (head-guard), a standard full-length race (similar to the race used with the FIRE system in studies at the University of Illinois), and a full-length race with a pneumatic gate. The authors characterized these races as affording low, medium, and high protection against disturbance of the feeding pig respectively. The results of this study, which are summarized in Table 2, suggest small difference in performance and feeding behavior between pigs on the system with the head-guard and the standard full-length race. However, animals using feeders equipped with the protective-race with the gate had fewer but longer feeding visits compared to the other two treatments (Table 2). This study suggests that using a protective race such as has been used in the University of Illinois studies will have minimal impact on performance and feeding behavior compared to designs of race that provide less protection.

Feed Intake Behavior

Computerized feed intake recording systems have been available commercially for less than 10 years and, therefore, research using such equipment has only been published over the last 5 years or so. To date most of the published research has been carried out in Europe, particularly in Holland, France and the United Kingdom. A summary of research results published to date using computerized feed intake recording systems is presented in Table 3. This table illustrates the tremendous variation in

the results of studies in feed intake behavior traits. For example, the number of daily feeder visits range from as low as 7 to as high as 73 with this range encompassing group sizes of 20 and individually penned pigs, respectively. Similarly, feed intake and feeder occupation time per visit range from 35 g and 1.4 min to 222 g and 6.9 min, respectively. Feed consumption rate, which has generally been defined as amount of feed consumed divided by the time spent in the feeder, ranged from as low as 15 g/min up to as high as 40 g/min (Table 3).

Growing-finishing pigs show a characteristic diurnal distribution in feeder activity an example of which is illustrated in Figure 2, which is taken from the study of Hyun et al. (1996). Visits to the feeder and feed consumption were greatest during the daytime, showing a characteristic peak between approximately 0600 h and 2000 h, and lowest during the nighttime (Figures 2a and 2b). The behavior of pigs in the feeder also showed a diurnal distribution with those pigs that visit the feeder during the peak in activity having shorter visits (Figure 2e), eating less per visit (Figure 2d), but having higher consumption rates (Figure 2f) than animals visiting the feeder during the nighttime. In this study (Hyun et al, 1996), the three sexes (boars, barrows and gilts) were compared and the results presented in Figure 2 suggest that the differences between barrows and gilts in feeding behavior were small. However, boars appeared to have more of their feeder visits and consume a bigger proportion of their total feed between 0700 h and 1600 h when activity at the feeder was greatest. This suggests that the boars were more successful at gaining access to the feeder when competition is highest.

Evidence of genetic variation in feeding behavior is shown in a small study carried out at this center by Hyun et al. (1996a) which compared purebred Yorkshire and Meishan barrows reared in mixed-breed groups of 10 pigs. The growth performance and feeding behavior of the two breeds was dramatically different (Table 4). The daily feed intake of the Meishans was approximately 1 kg lower than that of the Yorkshires and the Meishans made less than half the number of feeder visits but had a greater feed intake per visit compared to the Yorkshires (Table 4). In addition, the diurnal pattern of feeding behavior differed between the two breeds with Yorkshires consuming proportionately more of their feed at times of peak feeder activity (Figure 3b). It appeared that the Meishans were reluctant to compete for feeder access and, therefore, visited the feeder after the Yorkshires had consumed the bulk of their daily feed. Thus, a response of subordinate pigs in a group to increased competition for feeder access appears to be to eat at times of the day outside of the normal peak in feeding activity.

Individual Variation in Feeding Behavior

One of the striking features of daily feed intake behavior data is the tremendous variation observed both between individual animals and between consecutive days for the same animal. For example, the range in mean number of feeder visits per day for individual pigs of the same genotype, sex and weight was from 8 to 23 in the study of Hyun et al. (1996) and even greater (from 3 to 69 visits/day) in the study of Young and Lawrence (1994). Day to day variation in feed intake level in individual pigs is illustrated in Figure 4 where pigs from the study of Hyun et al. (1996) with high and low daily variation have been selected. It has been proposed that under commercial conditions feed intake could be measured on a daily basis and used to predict future feed intake. This information would be of value to producers in diet formulation. The data presented in Figure 4 raises questions about

how accurate such as approach might be.

Feed Intake Behavior and Energy Utilization

Any impact of variation in feeding behavior on the energy balance of the animal is likely to operate either through an increase in energy supply to the animal or through a reduction in energy utilization by the animal. There is evidence from Dutch research of a relationship between feeding behavior and nutrient digestibility. Thus De Haer and De Vries (1993a) found that 86% of variation in protein and dry matter digestibility was explained by variation in feed intake pattern in individual housed pigs. Correlations suggested that pigs that had a higher number of short visits and ate a lower proportion of large meals had higher digestibility coefficients. However, with animals in groups (8 pigs per group) the correlations between feed intake pattern and dry matter and crude protein digestibility were much lower and variation in feeding pattern accounted for only 20% of the variation in digestibility.

The impact of variation in feeding behavior on energy utilization has not been researched. It is possible, however, that pigs that have higher levels of feeder related activity will expend more energy in this respect. However, it is uncertain if their total energy expenditure will be any different from those with lower levels of feeder activity. Our studies have generally found low correlations between feeding patterns and growth rate, feed efficiency and carcass composition (Table 5). This suggests that, overall, any impact of feeding behavior on energy balance, is likely to be minimal under commercial conditions.

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Table 1. Effect of group size on growth performance and feed intake traits in growing pigs

	Group size (pigs/pen)					
	2	4	8	12	sem	SIG.
Daily feed intake (kg)	1.79[a]	1.75[ab]	1.67[c]	1.59	.039	**
Daily gain (g)	816[a]	785[ab]	755[bc]	719[c]	15.2	**
Gain:feed	.46	.46	.46	.46	.008	ns
Number of feeder visits per day	20.6	22.4	18.2	19.4	1.22	ns
Feed intake per visit (g)	98.0[ab]	86.8[a]	101.8[b]	94.5[ab]	5.42	**
Feeder occupation time per visit (min)	6.33	6.19	6.71	5.89	.321	ns
Feeder occupation time per day (min)	123.2[ab]	127.7[a]	112.1[bc]	99.0[c]	4.84	**
Feed consumption rate (g/min)	15.5[ab]	14.5[a]	15.5[ab]	16.5[b]	.57	**

Means in the same row with different superscripts differ (P<.05)
Hyun and Ellis (1996b)

Table 2. The influence of feeder-race design on growth performance and feeding behavior in growing pigs

	Feeder-race design			
	Head-guard	Standard Full-length	Full length with gate	sed
Degree of protection	Low	Medium	High	
Daily feed intake (kg)	2.06	1.94	1.89	13.0
Daily gain (g)	794	810	773	35.0
Feed conversion ratio	2.59	2.40	2.45	.048
Number of feeder visits per day	13.3	14.0	10.4	1.89
Feed intake per visit (g)	172[a]	157[a]	202[b]	11.1
Feeder occupation time per visit (min)	4.8[a]	4.8[a]	6.2[a]	.37
Feeder occupation time per day (min)	57.1	60.6	59.4	4.29
Feed consumption rate (g/min)	36.9[a]	33.2[b]	32.8[b]	.82

Means in the same row with different superscripts differ (P<.05)
Nielsen et al. (1995b)

Table 3 . Summary of studies using computerized feed intake recording equipment with growing-finishing pigs

Study	Feeding System	Genotype	Sex	Group Size	Liveweight Range (kg)	Diet Form	DFI (g)	ADG (g)	NFV	FIV (g)	FOV (min)	CR (g/min)	Treatment
Feddes et al., 1989	-			4	36 -	Meal	1350	-	-	-	-	15.2	Constant Temp 33°C
				4	36 -		1180	-	-	-	-	14.3	Cyclic (26 - 40°C
Xin &De Shazer, 1991	-	Crossbred	G	1	31 -	Meal	1700	810	10	170	13.3	-	Constant (31°C)
		Crossbred	G	1	31 -		1760	840	11	160	14.3	-	Cyclic (26 - 33°C)
		Crossbred	G	1	31 -		1530	700	9	170	13.5	-	Cyclic (23 - 40°C)
De Haer et al., 1992 IVOG	DL x DY	E & G		8	25 - 100	-	1992	659	18	137	3.9	34.9	
De Haer & Merks, 1992	IVOG	DL	E	1	25 - 100	-	2203		58.6	38	1.5	27.2	
		DL	E	8	25 - 100		2043		14.4	159	4.7	32.0	
De Haer & DeVries, IVOG 1993a	DL		E & G	1	25 - 100	-	2075	741	72.8	35	1.4	26.9	
	DL		E & G	8	25 - 100		1934	642	16.2	156	4.8	32.4	
De Haer & DeVries, IVOG 1993b	DL		E	8	25 - 100	-	1868	663	15.4	155	4.88	33.2	
	DL		G	8	25 -100		1879	608	15.9	151	4.56	31.5	
	DY		E	8	25 - 100		1854	713	18.8	134	3.3	37.9	
	DY		G	8	25 - 100		1862	651	21.7	109	3.0	36.9	
Labroue et al., 1994 ACEMA	FL		E	9-14	35 - 100	Pellet	2190	862	13.6	196	5.2	37.3	
	FL		G	9-14	35 - 100		2560	815	11.7	222	6.9	32.3	
	FLW		E	9-14	35 - 100		2150	882	26.2	146	3.5	40.1	
	FLW		G	9-14	35 - 100		2520	835	23.6	183	4.7	37.0	
Young & Lawrence, FIRE 1994	BLW x BL		E & G	10	32 - 69	Pellet	-	922	12	-	-	-	
Nielsen et al., 1995a FIRE	BLW x BL		E	5	34 -	Pellet	1456	695	15.9	96	4.3	23.8	
	BLW x BL		E	10	34 -		1609	762	13.6	135	5.0	26.9	
	BLW x BL		E	15	34 -		1416	714	13.4	127	4.6	27.0	
	BLW x BL		E	20	34 -		1495	721	7.1	214	6.9	31.6	
Nielsen et al., 1995b FIRE	BLW x BL		E	10	34 - 56	Pellet	2055	794	13.3	172	4.8	36.9	Low protection
	BLW x BL		E	10	34 - 56		1941	810	14.0	157	4.8	33.2	Moderate protection
	BLW x BL		E	10	34 - 56		1889	773	10.4	202	6.2	32.8	High protection

DFI =daily feed intake; ADG =average daily gain; NFV =number of feeder visits; FIV =feed intake per visit; FOV =feeder occupation time per visit; CR =feed consumption rate. DL =Dutch Landrace; DY =Dutch Yorkshire; FL =French Landrace; FLW =French Large White; BLW =British Large White; BL =British Landrace; E =boar; G =gilt.

Table 4. Comparison of Meishan and Yorkshire barrows for growth performance and feeding behavior

Items	Meishans	Yorkshire	Avg. SE	Sig.
Initial body weight (kg)	36.4	42.1	1.19	**
Final body weight (kg)	51.9	72.3	1.52	**
ADG (g)	369	721	21.0	**
Daily feed intake (kg)	1.37	2.34	0.067	**
Gain:Feed (kg/kg)	0.27	0.31	0.015	ns
No.of feeder visit per day	7.7	18.5	0.23	**
Feed intake per visit (g)	176.7	129.6	2.62	**
Feeder occupation time per visit (min)	12.9	7.4	0.23	**
Feeder occupation time per day (min)	82.8	114.3	1.67	**
Feed consumption rate (g/min)	14.8	19.3	0.17	**

ns, *, **:not significant, P<0.5, P<.01, resp.
Hyun and Ellis (1996a)

Table 5. Phenotypic correlations between feeding pattern and growth performance

	DFI[1]	ADG[1]	G:F[1]	Backfat thickness[2]
Number of feeder visits per day	-.28	-.13	.14	.07
Feed intake per visit	.70	.38	-.29	.12
Feeder occupation time per visit	.42	.11	-.31	.12
Feeder occupation time per day	.25	.02	-.24	.19
Feed consumption rate	.31	.32	.06	.002

[1]Hyun et al. (1996)
[2]Hyun, unpublished (1996)

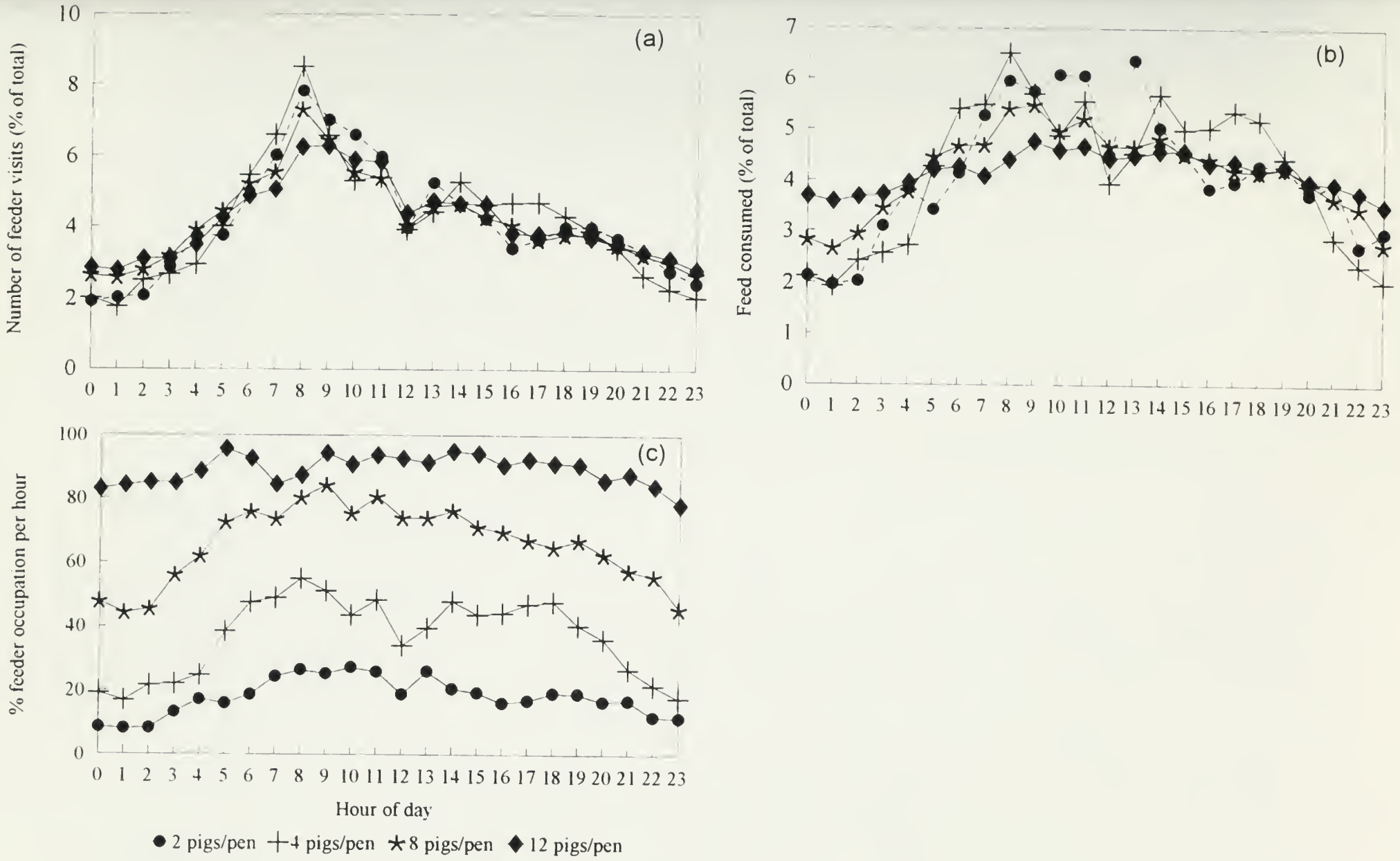

Figure 1. Diurnal distribution of feeder activity of pigs in four different group sizes; (a) number of feeder visits; (b) feed consumed; (c) percentage of feeder occupation time.
(Hyun and Ellis, 1996b).

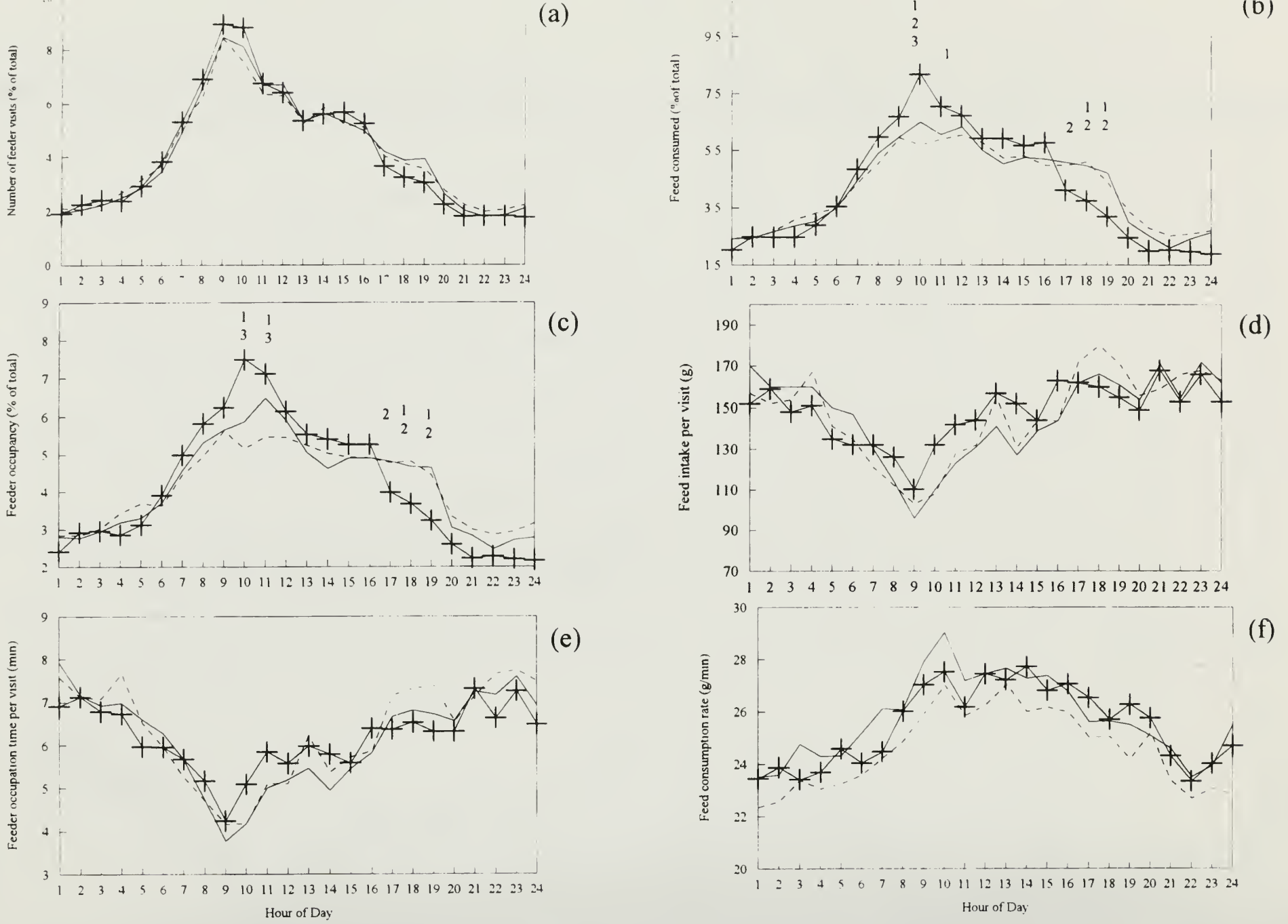

Figure 2. Diurnal distribution of feeder activity, boars (+) , barrows (-) and gilts (--); (a) number of feeder visit,; (b) feed consumed; (c) feeder occupancy; (d) feed intake per visit; (e) feeder occupation time per visit (f) feed consumption rate.
1 = boars and gilts differ ($P < .05$); 2 = boars and barrows differ ($P < 05$); 3 = barrows and gilts differ ($P < .05$).
(Hyun et al., 1996)

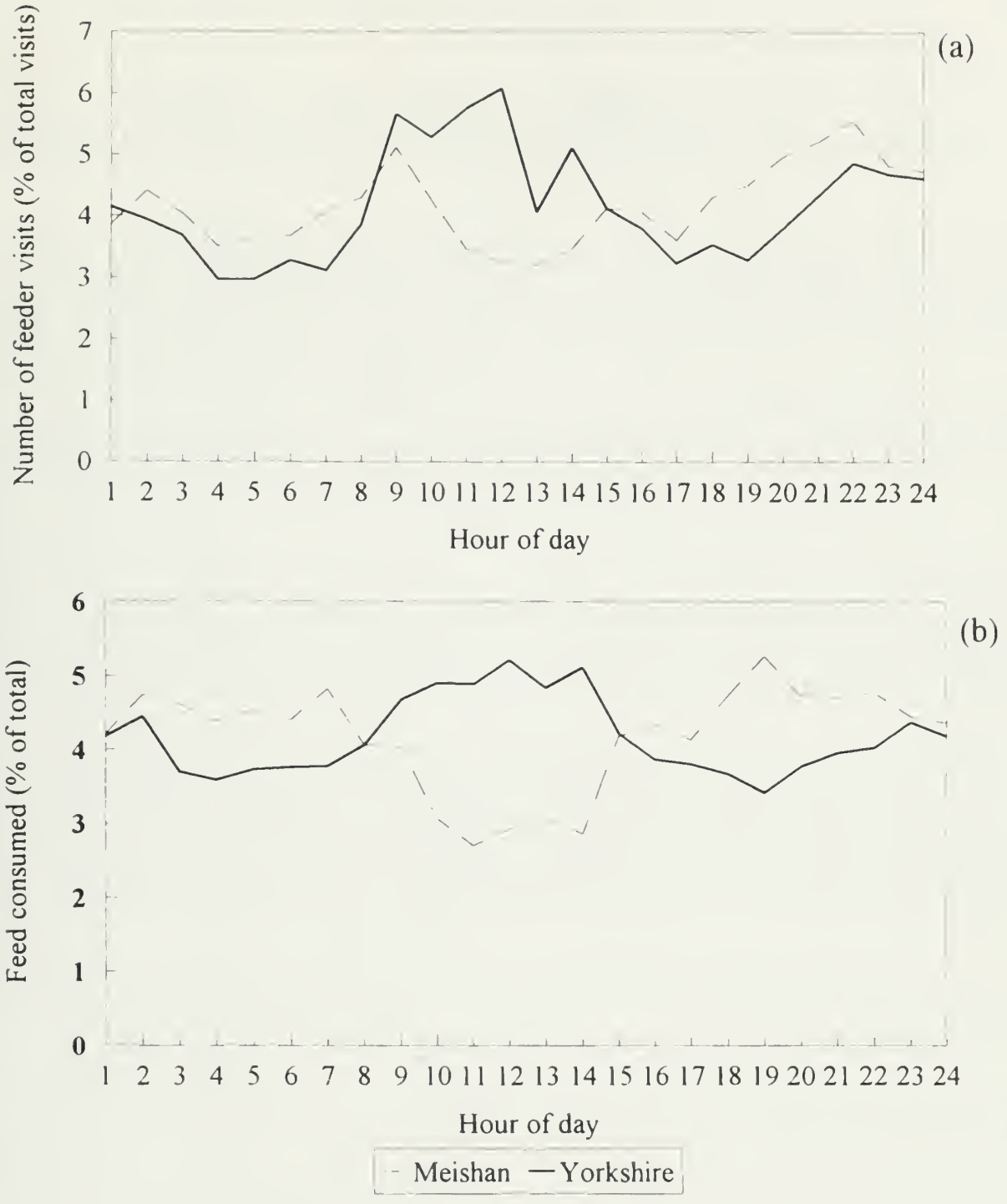

Figure 3. Diurnal distribution of feeder activity for Meishan and Yorkshire barrows: (a) Number of feeder visists; (b) Amount of feed consumed.
(Hyun and Ellis, 1996a)

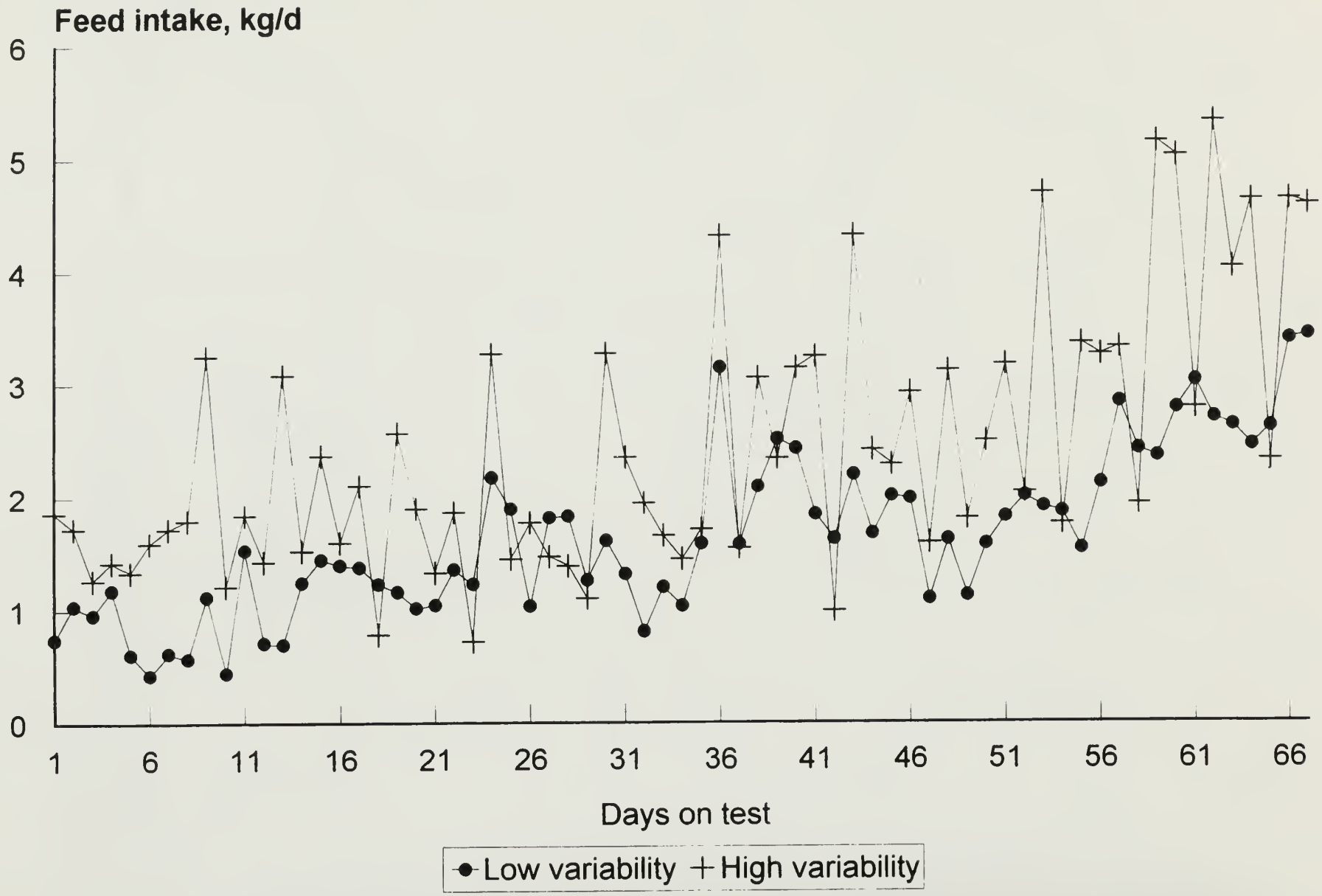

Figure 4. Daily feed intake variation in growing pigs.
(Hyun et al., 1996)

Strategies to Minimize the Loss of Metabolizable Energy to the Environment

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Pork producers continue to fine-tune their operations and practices so as to take advantage of available technology in their inexorable quest to maximize their economic opportunities. The cost of feed continues to be the major part of the cost of producing pork. The metabolizable energy in the feed is precious, as it is energy directly useful to a pig. Any metabolizable energy that is lost to the environment is an inefficiency.

In this paper, the origin and factors affecting the value of the metabolizable energy in the diet will be explored, and will serve as a prelude to discussing some practical strategies for minimizing the loss of metabolizable energy to the environment.

Whither dietary energy?

More complete discussions of a pig's partitioning and use of dietary energy are available elsewhere (NRC, 1981a; Ewan, 1991; Noblet, 1996). A brief review at the outset of this paper, however, will serve to set the stage for focusing on the primary topic here. Incidentally, although different authors are referring to the same phenomena and things, terminology and units still may vary among sources.

Dietary energy: from gross to digestible. The nutrients a pig ingests in a given period contain combustible chemical-bond energy that in sum comprises the **gross intake energy** (GIE). Not all of this energy is useful to the pig in metabolism. For example, the fecal excreta also contains combustible chemical-bond energy, called the **fecal energy** (FE), which is a considerable variable among feed ingredients and feeds. The difference, GIE - FE, is called the **apparent digestible energy** (ADE).

The **digestibility** of a diet — the ratio, ADE/GIE — is determined by factors such as

- the digestion coefficient of the pertinent feedstuffs (*e. g.*, much of a pig's dietary fiber is relatively indigestible),
- feed-intake rate (which tends to be negatively correlated with digestibility of dietary components), and
- organic materials originating in the digestive system *per se*.

These factors mostly fall in the realm of nutritional science.

Dietary energy: from digestible to metabolizable. The body excretes some of the apparent digestible energy for that period as the **combustible gas energy** (CGE) (usually negligible) and some as the **combustible urine energy** (CUE) (mostly in urea, an end-product of nitrogen metabolism). The difference, ADE - (CGE + CUE), represents that part of the GIE that the pig's cells can actually make use of — can actually "metabolize", and it is called the **metabolizable energy** (ME).

The **metabolizability** of the ADE — *i. e.*, the ratio, ME/ADE — for a pig consuming a nutritionally appropriate diet typically is ~.96. But this value does vary slightly due to factors such as dietary protein concentration and balance of amino acids, both of which are determinants of UE. These factors also tend to fall in the realm of nutritional science.

Whither metabolizable energy?

The fundamental partitioning: ME = NPE + MH. Other approaches are usually taken by nutritionists, but it is convenient for present purposes to consider that the ME ultimately becomes partitioned between two things:

- the **net product energy** (NPE) — *e. g.*, **carcass energy** (CE), **conceptus mass energy** (CME), or **milk energy** (ME), and

- the **metabolic heat** (MH) — which is lost to the environment, and hence wasted, unless the pig needs it to keep its body warm.

In other words: ME = NPE + MH. A goal of pork production is to maximize the very important ratio, NPE/ME, which reflects the overall efficiency with which ME is being converted to agricultural product. *The complement of this ratio, of course, is the inefficiency ratio, MH/ME, which reflects the loss of precious ME to the environment.*

But there is more to it. Whether or not the bipartite-fates-of-ME approach just mentioned is convenient, it turns out to be a bit too simplistic for purposes of making management decisions in pork production:

- For one thing, **environmental adaptates** — a pig's homeokinetic responses to adverse or extreme environmental conditions — increase its total NME requirement, which equals the animal's **standard metabolic rate** (SMR = 70 $W^{.75}$ kilocalories daily [where W = body weight in kilograms]) plus any and all additional energy expenditures associated with individual survival. *The NME, in its entirety, ultimately is lost as heat to the environment.*

- For another thing, the greater a pig's productive rate,

    - the smaller the *portion* of its ME that must be used as NME — *i. e.*, the smaller the inefficiency ratio, NME/ME,

    - hence the greater the portion of ME that can show up as NPE — *i. e.*, the larger that important efficiency ratio, NPE/ME.

Delving further into the matter

Once all the numerous fates of ME come to be accounted for, several of the factors that determine the pig's partitioning of ME in agricultural settings can be strategically manipulated in economical ways so as to enhance that important efficiency ratio, NPE/ME — and hence to enhance profitability of the enterprise. The efficiencies of the **net uses** of ME for bodily maintenance (NME) and for agricultural product (NPE) are determined by some factors that fall in the realm of genetic science, and some others that fall in that of environmental science. Again, there are available (*e. g.*, Ewan, 1991; Noblet, 1996) more complete discussions of the fates of ME in a pig's body, including:

- the inherent inefficiency of the various maintenance processes — ~.75-efficient net use of ME as NME, and

- the inherent inefficiency of growth processes — ~.40- to .70-efficient net use of ME as NPE for growth (depending on composition of growth [Kielanowski, 1972; Reeds *et al.*, 1993]) (mean .63-efficient [Boyd and McCracken, 1980]).

The inevitable consequences of these metabolic inefficiencies show up as heat: the **heat increment of maintenance HIM** and the **heat increment of production HIP**, respectively, and ordinarily they are part of the heat that is lost to the environment.

Opportunities are with NME

The MH — the metabolic heat, and the heat that is lost to the environment — equals the sum of the NME, the HIM, and the HIP. That is, MH = NME + HIM + HIP. Any strategy intended to minimize the loss of ME as heat to the environment must involve NME, HIM, or HIP. The HIP is directly proportional to the NPE, so — apart from enhancing metabolic efficiency — a reduction in HIP would necessarily be associated with a reduction in NPE, which would be counterproductive.

Opportunities to reduce the loss of ME as heat to the environment will have to do instead with the NME and its associated HIM. For instance:

- Bodily maintenance — tantamount to individual survival processes, which create the demand for NME — is any animal's very top vital priority. Usually, any and all maintenance needs — including both standard and extraordinary energy expenditures — will be satisfied *before* productive processes will be supported, or, at least, *fully* supported.

- Among other things, extreme physical activity and adapting to stressors of any and all kinds — *e. g.*, disease defenses, heat to keep the body warm in either normothermic or febrile states, coping with frustration and other emotional states derivative from stressful physical and social environments — all fall in the category of maintenance activities. They all are supported by NME, hence they draw upon the ME pool, in effect redirecting ME away from productive processes, diminishing that important efficiency ratio, NPE/ME.

- The greater a pig's feed-intake rate, the more of the ME that will remain after NME requirements have been fulfilled, to be used in productive processes. In other words, increasing feed-intake rate, in effect, increases also that important efficiency ratio, NPE/ME, while decreasing the inefficiency ratio, NME/ME.

- Ironically, however:
  - the ratio, ADE/GIE, is negatively correlated with feed-intake rate and
  - the leaner the carcass growth, apart from the carcass's being more desirable and valuable in today's consumer climate, the less efficient will be a pig's conversion of ME to NPE (Kielanowski, 1972).

The crux of plausible strategies

Clearly and simply, management strategies that either

- enhance a pig's dietary-energy intake or

- minimize the need for a pig to cope with or adapt to any adverse or extreme facet of its environment

will tend to increase the efficiency with which ME is converted to NPE, thus minimizing the inefficiency ratio, NME/ME, and with it the loss of ME as heat to the environment.

Genetic and environmental-design effects on dietary-energy intake are addressed elsewhere in the proceedings of this conference (Ellis, 1996; Curtis, 1996), and likewise some aspects of coping with and adapting to stressors (*e. g.*, disease and social tension) (Johnson, 1996; Curtis, 1996). Strategies to optimize those factors, of course, inherently work to minimize the loss of ME as heat to the environment. Remaining to be discussed are strategies related to physical activity, heat to keep the body warm, and hot-environment-induced reduction in feed-intake rate, respectively.

Physical activity

Provided the thermal environment is neither too cool nor too warm, most of a pig's NME will be determined by the needs of the vital organs in the core of the body. Unless physical activity is extreme — *e. g.*, walking several kilometers daily — physical activity ordinarily amounts to relatively little additional energy expenditure. Growing-finishing pigs residing in an intensive production system spent ~80 percent of each 24-hour period sitting or lying, and even when offered environment-enriching features (including a ramped mezzanine) with which to interact, the pigs spent <10 minutes daily doing so (Pedersen *et al.*, 1997a). Moreover, whereas the SMR of a pig weighing 50 kilograms is ~1880 kilocalories daily, this same pig would expend only ~300 kilocalories — *i. e.*, ~15 percent of the SMR — walking 6 kilometers (Tucker, 1969). Yet growing-finishing pigs spent only ~1.5 hours daily moving (walking or running) (Pedersen *et al.*, 1997a).

Production systems that necessitate the pigs' engaging in considerable physical activity presumably will have little effect on either NME requirement, ME lost as heat, or growth rate (Pedersen *et al.*, 1997b). Moreover, strategies that would aim to minimize physical activity would seem to be of little or no benefit in terms of minimizing loss of ME as heat to the environment.

Heat to keep the body warm

The greatest opportunity in the North American pork industry to reduce the loss of ME as heat to the environment has to do with providing the pigs a comfortable thermal environment during periods of cool and cold weather. Even two decades after knowledge of these relationships began being published, it is not being routinely applied at many pork-production operations.

When a pig's **effective microenvironmental temperature** falls below the **lower critical temperature**, by definition, the animal must increase its MH production rate above the thermoneutral level in order to meet its need for heat to keep the body warm (NRC, 1981a,b; Curtis, 1983, 1985b). Either the pig will increase feed-intake rate, decrease NEP, or both — all counterproductive measures — to fulfill this top-priority need for NME. In any case, that important efficiency ratio, NPE/ME, will be reduced, and consequently a greater portion of ME will become MH and be lost as heat to the environment.

Factors determining effective microenvironmental temperature. The heat budget of a growing-finishing pig depends on several thermal factors besides air temperature (Mount, 1975). For pigs in small groups, *e. g.*, a 20 centimeter per second increase in air speed at pig level is equivalent to an ~1 C° decrease in environmental temperature, and 45 centimeters per second to 1.5 C°(Verstegen and van der Hel, 1976). Pigs weighing 23 kilograms at the start were residing in small groups at an air temperature of 12°C, and as microenvironmental air speed rose from 10 to 45 and on to 80 centimeters per second, average daily body-weight gain fell from .57 to .50 and on to .43 kilogram (Mount *et al.*, 1980).

The nature of the floor also affects effective microenvironmental temperature. Of course, pigs can adjust individual and group posture greatly in response to changes in the thermal environment (Grommers *et al.*, 1970; Boon, 1981). Despite this, 40-kilogram pigs residing on a solid concrete floor experience an environment that is ~7.5 C° cooler than when on straw bedding, and this is reflected in a significant reduction in feed-conversion efficiency (Verstegen and van der Hel, 1974; Verstegen *et al.*, 1977).

Lower critical temperature. Group-reared pigs with *ad-libitum* access to feed have a lower critical air temperature of ~13°C during the growing period, ~10°C during finishing, assuming there is little air movement and that wall, ceiling, and floor temperatures are close to that of the air (Verstegen *et al.*, 1978; Bruce and Clark, 1979). But in most agricultural settings the effective temperature is below the air temperature (Mount, 1975; Curtis, 1983).

Productive performance of pigs in the cold. Pigs fed at a constant rate gain ~10 grams less each day per degree Celsius of coldness during the growing period, ~25 grams less daily during finishing (Verstegen *et al.*, 1979). During the growing period (25-60 kilograms body weight), pigs need ~25 grams of extra feed per day per Celsius degree of coldness to raise the rate of body-weight gain to the thermoneutral level, and finishing pigs (60-100 kilograms) require ~40 grams per day per degree (Verstegen *et al.*, 1982).

Weanling pigs. Of course, a weanling pig is even more sensitive to cool and cold environments. The lower critical microenvironmental temperature of *ad-libitum*-fed pigs the first few days after weaning is ~28°C, and MH production rate rises by ~12 kilocalories daily per Celsius degree effective microenvironmental temperature lies below this point (Le Dividich *et al.*, 1980). By the time a young pig has reached a body weight of 15 kilograms, its lower critical temperature might be as low as 21°C (Close, 1981). A 20-kilogram pig consuming ME at a rate 3 times the thermoneutral maintenance level has a lower critical microenvironmental temperature of ~15°C, and must increase its MH production rate by ~40 kilocalories daily per Celsius degree of coldness it is experiencing (Mount, 1972).

Hot-environment-induced reduction in feed-intake rate

Warm and hot environments affect the performance of growing-finishing pigs by lowering the feed-intake and growth rates (NRC, 1981b; Curtis, 1985a). Of course, when this happens, the amount of ME remaining, after the requirements for NME have been fulfilled, is reduced, so NPE as well as that important efficiency ratio, NPE/ME, are reduced.

An environmental temperature range of 18-21°C generally has been found to support optimal productive performance of growing-finishing pigs, and these animals typically consume 60-100 grams daily less feed and gain 36-60 grams daily less body weight for each Celsius degree the mean daily environmental temperature lies above 21°C (Curtis, 1985a).

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Are We Still Having Vitamin E and Selenium Deficiencies in Pigs?

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Summary

Although most commercial feed companies are currently fortifying their swine diets with the maximum allowable limit of inorganic Se (.3 ppm) and relatively high dietary vitamin E levels, the vitamin E-Se deficiency is still occurring on many swine farms. The periods where the deficiency is more likely to occur is in the neonate, at weaning, and during the reproductive period. It has been demonstrated colostrum and milk vitamin E and Se concentrations decline with advancing age and therefore older high producing sows are more likely to produce progeny with a low vitamin E and Se status at birth and weaning than younger sows; and postweaning pigs will encounter the deficiency more quickly if their vitamin E and Se status is compromised prior to weaning. High dietary vitamin E levels and the use of organic Se during the 3 critical periods when the deficiency onset is most frequently encountered appears effective.

Introduction

During the 1960's, the occurrence of the vitamin E-Se deficiency was prevalent on many swine farms. The deficiency was predominately evident in the postweaning pig where mortalities were often as high as 10%. Sows exhibited deficiency symptoms with a lower litter size, fetal deaths, prolonged farrowing times, poor milk let down, high incidences of MMA, and weak lethargic pigs at birth, whereas younger pigs had white muscle, mottled livers, ceroid pigment in fatty tissue, and the death of rapidly growing pigs. Although many factors contributed to the onset of these nutritional deficiencies, perhaps the one factor that had the greatest effect was the movement of pigs to complete confinement. The effect of feeding sows in confinement or pasture on the sow and pig's status of these nutrients was demonstrated by Mutetikka and Mahan (1993). Gilts fed a nonfortified Se and vitamin E diet on pasture had a 300% higher milk α-tocopherol content and a 75% higher Se content than females fed the same diet in confinement (Table 1). The progeny from pasture fed sows were therefore in a better vitamin E and Se status at weaning (Table 1): the period where the deficiency onset is greatest.

With the subsequent approval of dietary inorganic Se (sodium selenite or selenate) at .3 ppm by FDA (1987) and with diets being fortified with high dietary vitamin E levels by commercial feed companies, the deficiency occurrence has been reduced in all phases of swine production, but not eliminated. The intent of this paper is to examine the conditions today which may precipitate the

deficiency, and then to evaluate the desired dietary level and sources of these nutrients to be used for the swine herd.

Prenatal Nutrition Effects

Vitamin E. Dietary vitamin E fed to the pregnant sow does not effectively transfer to the developing fetus (Mahan, 1991). Fetal liver is the predominant organ containing α-tocopherol and although the neonatal pig does have a somewhat higher vitamin E content when supplemented levels of this vitamin are provided to the sow, the liver α-tocopherol in the neonate is low (Table 2). Consequently, the pig is born at a low vitamin E status (i.e. in reality it is born deficient in vitamin E) and is susceptible to the deficiency onset postnatally (Table 2).

Selenium. Selenium on the other hand can be transferred across the placenta to the developing fetus. The experiment of Mahan et al. (1977) demonstrated that neonatal pig tissue and serum Se concentrations increased when the sows supplemental dietary Se level increased from 0 to .5 ppm (Figure 1). The total quantity of Se deposited is low in the neonate, being about .07 mg Se per pig at birth (Figure 2: Mahan, unpublished data). Selenium transfer to the fetus is higher, however, when an organic Se source is fed improving the pig's Se status at birth (Table 3; Mahan and Kim, 1996).

Postnatal Nutritional Effects on Sow and Progeny

Vitamin E. The source of vitamin E for the neonatal pig is colostrum. Because the pig is born at a low vitamin E status, the neonatal pig is dependent upon α-tocopherol from this exogenous source in order to prevent free radical damage to body cellular tissue. Loudenslager et al. (1986) demonstrated the antioxidant protective role of α-tocopherol in neonatal pigs when intramuscularly injected with 200 mg of Fe (i.e. Fe being a prooxidant). Their results demonstrated that pigs injected with Fe, had serum α-tocopherol concentration which declined postinjection, whereas those not injected with Fe had higher serum α-tocopherol levels (Table 4).

Colostrum has an extremely high α-tocopherol content and therefore is an excellent source of vitamin E for the neonatal pig. Colostrum α-tocopherol concentration increases when either the dietary level of vitamin E fed to the sow is increased (Table 5) or when vitamin E is injected during late gestation (Chung and Mahan, 1995). Although mature milk has a lower α-tocopherol content than colostrum, it is also an excellent source of vitamin E with its α-tocopherol content increasing as the dietary vitamin E level fed to the sow is increased (Table 5). Blood serum α-tocopherol content of the neonatal pig is initially low, but increases dramatically after the consumption of colostrum, and continues high throughout lactation (Figure 3). This suggests that both milk sources have a high bioavailability of the nutrient for the suckling pig.

When the sow is fed inadequate dietary vitamin E and(or) her body fat stores are low which depletes her body vitamin E stores, the resulting concentration of vitamin E in colostrum and milk will be reduced. Consequently, the α-tocopherol content of sow milk declines with advancing parity (Mahan, 1991). Pigs of older sows may therefore not receive as much vitamin E in their milk supply and are more prone to the deficiency upon weaning.

Selenium. Colostrum has a higher Se content than later milks and increases as the dietary Se level is increased. The provision of an organic Se source results in higher milk Se contents (Table 3; Mahan and Kim, 1996). The bioavailability of Se in sow milk to the nursing pig is high because of the resulting high serum Se content of the suckling pig (Figure 1), but is higher when an organic Se source is fed (Table 3).

Figure 3 demonstrates that the Se content of the nursing pig increases dramatically from birth to weaning, attributable to its retention from the milk supply. Pigs which nurse for a longer time will obviously retain more Se than those weaned early. This suggests that as early weaning pig programs are implemented on many swine operations, the accumulation of Se would be lower and the deficiency onset would more likely occur.

Sow milk Se content is affected by sow age. Figure 4 demonstrates that when sows were fed .3 ppm Se as sodium selenite, the resulting milk Se contents were highest in parity 1 and 2, whereupon a decline occurred during the latter parities. This demonstrates that less Se transferred to mammary tissue of older sows. Consequently, the pigs of mature sows are more likely to enter the postweaning period at a lower Se status than the progeny of younger sows.

Postweaning Period

Young pigs enter the postweaning period with a variable Se and vitamin E tissue status which depends on those several factors which affect the sow (Tables 1 and 2). Upon weaning, a rapid decline in pig serum and tissue Se and α-tocopherol concentrations occurs (Figure 1 and 2). It is during these initial weeks postweaning that the deficiency is most frequently encountered in young rapidly growing pigs. Although mortalities of 10% are generally not encountered today as they once were, it is quite common that a 1 to 2% death rate occurs in the nursery, some of which can be attributable to a deficiency of either or both nutrients. The most common clinical deficiency symptoms that occur today is the sudden death of large rapidly growing pigs, the presence of mulberry heart, and a large accumulation of fluid in the pericardial sac. In our own swine research herd at Ohio State University, it has become essential to inject pigs at weaning with Se and vitamin E to prevent the sudden death problem during the postweaning period.

Although high dietary levels of Se and vitamin E are routinely added to many commercial starter diets, the occurrence of the deficiency is still prevalent on most swine farms. Currently, only

inorganic Se can be added to swine diets at a .3 ppm level. The supplemental level of vitamin E in most commercial starter feeds in the United States and Europe is 6 to 10 times the current NRC (1988) recommendations in an attempt to prevent the observed deficiency problem.

One possible reason for the deficiency onset is the relatively poor absorption of synthetic vitamin E compounds by the weaned pig, at least to 4 week postweaning. Figure 5 presents information demonstrating the decline in serum tocopherol within 1 week of weaning, but there was no difference in serum tocopherol concentrations during the following weeks postweaning even when vitamin E supplemented the starter diet.

Although Se may be added at a dietary level of .3 ppm (FDA), there is evidence to suggest that inorganic Se may not be as effectively retained by the pig as organic Se. Inorganic Se is clearly effective for glutathione peroxidase production, but beyond that much of the inorganic Se may be voided in the urine and not effectively stored.

The vitamin E and Se status of the pig at weaning will indeed influence when and if the deficiency occurrence will be encountered postweaning. Table 6 demonstrates that when dietary Se is fed to the sow the onset of the deficiency in the progeny was affected. The occurrence of the Se deficiency was more prevalent from those progeny with sows fed low dietary Se levels; whereas, when progeny were from sows fed supplemental Se the deficiency onset was not encountered as quickly postweaning. Table 7 generally demonstrates the same responses with sows fed varying levels of vitamin E. Sows fed low vitamin E diets had progeny which encountered higher incidences of the deficiency within 28 days postweaning, whereas, when sows were fed higher dietary vitamin E levels the progeny did not encounter the deficiency. Consequently, both sets of data clearly demonstrate that the vitamin E and Se status of the weaned pig will clearly influence the time when and if the deficiency will occur.

Reproduction and Immunity

The above results clearly demonstrate that vitamin E and Se deficiencies can occur in young swine and that the deficiency is most likely prior to or immediately after the nursing period. This suggests that the sow is not provided an adequate level of these nutrients and depletes her tissue of the nutrients. The question arises as to what would be the desired dietary levels of both nutrients that should be provided in the sows diet that would prevent this problem, whether either nutrient will influence the sow's reproductive performance, and what effect will either nutrient have on the sow or the pig's health .

Two experiments with varying levels of vitamin E fed over several parities have been conducted. Both studies reported in Table 8 demonstrated that litter size increased to a supplemental dietary level of 33 to 44 IU per kg diet.

Other reproductive benefits have been observed from supplemental vitamin E and Se by improvement herd health and the sow's immune response. Research conducted by Whitehair and Miller (1985) demonstrated that diets low in Se and vitamin E precipitated a high occurrence of MMA, whereas when these nutrients were supplemented, the disease malady was eliminated (Table 9). A 5 parity sow study evaluating increasing levels of vitamin E demonstrated that the incidence of MMA was lower as dietary vitamin E levels increased (Table 8; Mahan, 1994).

The effectiveness of both vitamin E and Se in increasing the humoral immunogenic response in pigs was demonstrated in 1980 by Peplowski et al. (Figure 6). Their results demonstrated that weanling-grower pigs either injected or fed both nutrients had a higher humoral antibody response than when either nutrient was provided independently.

Cellular immunity also appears to be enhanced from the combination of both nutrients. Larsen and Tollersud (1981) demonstrated that pig lymphocytes responded to both Se and vitamin E in a Phytohaemagglutinin response (Table 10). A recent study by Wuryastuti et al. (1993) demonstrated that pregnant gilts at 90 days postcoitum and (or) within 3 days postpartum had improved cellular immune responses when supplemental vitamin E (60 IU/kg) and Se (.3 ppm) were jointly provided (Table 11). Cellular immunity responses were increased in the colostrum and milk in response to both nutrients (Table 12). The efficacy of both nutrients appears to enhance the immunogenic response in sows. High dietary levels of approximately 60 IU vitamin E/kg and .3 ppm Se both appear necessary to maximize the immunogenic capability and to maintain herd health in adult reproducing sows.

Dietary Sources and Recommendations

The biologically active form of vitamin E in animal tissue is α-tocopherol. Although plant oils contain various tocopherol isomeres, the α form can be isolated and subsequently stabilized by adding an acetate to the active site on the molecule (d α-tocopheryl acetate). Synthetic vitamin E contains a mixture of 8 isomeres, also stabilized with acetate, but the combined activity of the isomeric mixture is expressed in the biologically active form (dl α-tocopheryl acetate). Each activity is expressed in international units (IU) and reflects the amount of the product which will reduce fetal atrophy in the gestating rat. The biological activity of each compound is presented in Table 13 and uses dl α-tocopheryl acetate as the reference standard.

Although substituting various vitamin E products on an equivalent IU basis should yield the same results, research conducted with weanling swine (Chung and Mahan, 1992) and with gestating sows (Mahan, unpublished data) suggests that natural α-tocopherol may have approximately 30% higher IU activity compared to its assigned activity (Table 13). However, because synthetic vitamin E (dl α-tocopheryl acetate) is the most widely used form in commercial feeds, the recommendations below reflect the use of that product.

Selenium sources have quite variable responses, but mainly when comparing organic vs inorganic sources. Inorganic Se (sodium selenite or selenate) is currently the only approved form for incorporation into livestock diets in the United States. Grains, animal products, and a Se enriched yeast source contains Se in one of several amino acid analogs, but the principle one is selenomethionine in the grain and yeast product. There is evidence suggesting that the pig does not effectively utilize inorganic Se above .1 to .2 ppm with higher dietary concentrations being voided largely in the urine. In contrast, organic Se when fed at higher dietary Se levels are more effectively retained, principally in the proteinaceous tissue of the body. Organic Se sources appear to be more satisfactory for reproducing animals, particularly since this form of Se is more effectively transferred through the placenta and mammary tissue of adult swine: the period when young pigs are most prone to the deficiency onset.

From the above discussion, the following recommendations for both vitamin E and Se would appear appropriate (Table 14). These recommendations reflect a relatively high vitamin E dietary level particularly for those periods where critical deficiency symptoms are likely to occur, enhanced reproductive performance and herd health conditions. Although the Se yeast product (Sel-Plex 50) is not currently approved for use in the United States, it's value for the reproducing animal appears excellent and should be considered as the main dietary source of Se for replacement and reproducing once approved.

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Table 1. *Effect of vitamin E and Se fortification in sow diets under various housing conditions on milk and pig tissue concentrations at weaning*[a]

Supplemental E/Se:	None			NRC (1988)
Item Housing:	Confinement[b]	Pasture[b]	Pasture/Confinement[c]	Confinement[b]
No. sows	7	6	6	8
Sow serum (weaning)				
α-tocopherol, μg/mL	.463	1.755	.663	1.073
Se, ppm	.107	.119	.098	.235
Milk (weaning				
α-tocopherol, μg/mL	.276	1.274	.334	.485
Se, ppm	.028	.049	.019	.058
Pig liver (weaning)				
α-tocopherol, μg/mL	.850	3.56	1.26	2.30
Se, ppm	.305	.394	.291	.394

[a]Source: Mutetikka and Mahan (1993).

[b]Housing condition during both gestation and lactation.

[c]Housing condition during gestation was pasture and in confinement (farrowing pens) during lactation.

Table 2. *Effects of sow dietary vitamin E levels on neonatal and weanling progeny Serum and tissue responses*[a]

Item	Sow Dietary Vitamin E (IU/kg) 0	16	33	66	SEM
			Neonate, 0-day		
Serum, no. litters	30	23	20	25	--
α-tocopherol, μg/mL	.050	.101	.164	.164	.010[b]
Liver, no. Pigs	12	12	14	14	--
α-tocopherol, μg/mL	.142	.224	.305	.305	.026[b]
Se, ppm	.191	.156	.171	.171	.019
			Weanling, 28-day of age		
Serum, no. litters[d]	30	28	25	24	--
α-tocopherol, μg/mL	.650	1.154	1.329	2.364	.120[b]
GSH-Px, units/mL[c]	.890	.766	.872	.878	.035
Liver, no. pigs	12	10	12	12	--
α-tocopherol, μg/mL	1.398	1.962	2.967	3.411	.269[b]
Se, ppm	.509	.484	.483	.481	.041

[a]Source: Mahan (1991)

[b]Linear response ($P < .01$).

[c]One unit equals 1 nmole NADPH oxidized/minute.

[d]There pigs per litter were bled and the serum samples pooled.

Table 3. *Effect of dietary selenium level and selenium source fed to reproducing gilts on progeny selenium status at birth and weaning*[a]

Item	Se Source:	Sodium Selenite		Organic Se[b]		SEM
	Se Level, ppm:	.1	.3	.1	.3	
				Neonatal Pig		
No. pigs		10	9	10	7	--
Liver Se, ppm		.236	.250	.283	.310	.031
Loin Se, ppm		.039	.055	.068	.085	.005[cd]
Sow milk Se (21-d), ppm		.041	.044	.051	.090	.003[e]
				Weaning Pig, 21-d		
No. pigs		8	6	6	7	--
Liver Se, ppm		.352	.388	.353	.509	.032[cd]
Loin Se, ppm		.101	.121	.129	.244	.021[cd]
Serum Se, ppm		.062	.075	.082	.102	.005[d]

[a]Source: Mahan and Kim (1996).

[b]Organic Se from Se enriched yeast.

[c]Dietary Se level response ($P < .01$).

[d]Se source response ($P < .01$).

[e]Se level x Se source interaction ($P < .05$).

Table 4. *Effect of sow vitamin E and selenium supplementation and iron injection on plasma antioxidant status of pigs*[a]

Item and Day of Age	Sow diet Basal	+ E + Se	SEM
Plasma tocopherol, μg/mL			
0-day	.13	.27	.19
2-day (200 mg Fe)	2.24	4.36	7.92[b]
2-day (0 Fe)	2.45	5.22	7.92[b]
21-day	1.58	2.19	3.56
Plasma GSH-Px, units/mL			
0-day	.13	.18	.02
2-day (200 mg Fe)	.19	.27	.02[c]
2-day (0 Fe)	.17	.24	.02[c]
21-day	.40	.50	.06
Plasma Se, ppm			
0-day	.037	.053	.002
2-day (200 mg Fe)	.044	.071	.001[b]
2-day (0 Fe)	.040	.065	.001[b]
21-day	.054	.096	.001[c]

[a]Source: Loudenslager et al. (1986).

[b]Significant response ($P < .01$).

[c]Significant response ($P < .05$).

Table 5. *Effect of sow dietary vitamin E levels on colostrum and 21-day milk tocopherol content*

	Dietary Vitamin E (IU/kg)					
Period	0	16	22	33	44	66	SEM
				Experiment I[a]			
Colostrum	2.37	4.32		8.02		7.88	1.0[b]
28-d Milk	.42	.75		1.25		1.66	.10[b]
				Experiment II[c]			
Colostrum			8.42		10.58	12.82	.78[b]
21-d Milk			1.92		2.54	2.96	.12[b]

[a]Each mean represents 15 to 24 observations averaged over a 3 parity period (Mahan, 1991).

[b]Linear response ($P < .01$).

[c]Each mean represents 70 to 90 observations averaged over a 5 parity period (Mahan, 1994).

Table 6. *Effect of sow dietary Se levels on deficiency onset in the progeny postweaning (28 day).*

Item	Sow dietary Se	
	Control	.1 ppm Se
	Parity 1	
Pig serum Se, ppm		
0 (weaning)	.020	.047
14-d	.012	.038
28-d	--[a]	.030
42-d	--[a]	.016[b]
	Parity 2	
Pig serum Se, ppm		
0 (weaning)	.022	.067
14-d	.017	.030
28-d	.014	.021

Source: Mahan et al., (1975)

[a]Pigs were removed from trial due to Se deficiency symptoms (white muscle; cardiac fluid accumulation, gastric ulcers).

[b]Pigs demonstrated Se deficiency symptoms.

Table 7. *Effect of sow dietary vitamin E level on deficiency onset in progeny postweaning (28 day).*

Item	Sow Dietary Vitamin E Level, IU/kg				
	0	16	33	66	SEM
No. pigs killed	15	13	12	14	--
Deficiency symptoms, %					
Ceroid pigment	33	15	0	0	3[a]
Esophagogastric ulcers	13	0	8	7	3
Heart fluid accumulation	20	23	17	7	3
Serum α-tocopherol, μg/mL	.372	.428	.451	.523	.026[a]
Liver α-tocopoherol, μg/g	.646	.705	.827	.823	.050[a]

Source: Mahan (1991).

[a]Linear response.

Table 8. *Effect of dietary vitamin E on sow reproductive performance and the incidence of mastidis, mastitis, agalactia (MMA).*

	Dietary Vitamin E (IU/kg)						
Period	0	16	22	33	44	66	SEM
				Experiment I[ab]			
No. Litters	26	30		30		26	--
Pigs/litter, no.							
Birth	9.85	10.87		11.20		10.04	.48
7-day	7.67	8.43		9.04		9.28	.4
28-day	6.73	7.00		7.88		8.14	.5
				Experiment II[de]			
No. Litters			134		123	120	--
MMA Score (0-3)[c]			.26		.09	.08	.05[f]
Pigs/litter, no.							
Birth, total			11.85		11.97	12.27	.27[f]
Birth, live			11.45		11.66	11.60	.26
7-day			9.77		9.86	9.80	.21
28-day			9.39		9.51	9.28	.18

[a]Average over 3 parities.
[b]Source: Mahan (1991).
[c]A score of 0 = no problem; 3 = severe problem.
[d]Average over 5 parities.
[e]Source: Mahan (1994).
[f]Quadratic response ($P < .05$).
[g]Linear response ($P < .01$).

Table 9. *Responsiveness of gilts to vitamin E-Se supplementation on various postpartum measurements*[a]

Item	High Moisture Corn[b] BASAL	BASAL + Se + E	SEM
No. Gilts	10	9	--
Clinical MMA, no.	5	0	--
Litter			
Pigs born, no.	8.8	10.9	.7
Weight, birth	11.2	15.2	.9[c]
Weight, 21-day	31.4	45.1	3.4[c]
Weaning, %	80.2	86.8	5.7
Litter Gain (9-21 d)	20.2	29.9	--

[a]Source: Whitehair and Miller, 1985.

[b]Treatment response ($P < .05$).

[c]High moisture corn dried prior to being fed.

Table 10. *Effect of dietary vitamin E and Se on pig lymphocyte response to phytohaemagglutinin.*

Dietary Treatments		PHA Response
Se (ppm)	Vitamin E mg/day	(log)
0	0	.97
0	40	1.88
.05	0	1.65
.05	40	2.16
.10	0	1.31
.10	40	1.68

[a]PHA = Phytohaemagglutinin.

Source: Larsen and Tollersud (1981).

Table 11. *Effect of vitamin E and selenium deficiency on blood lymphocyte blastogensis, blood polymorphonuclear cell (PMN) phagocytic activity and PMN microbicidal activity*[a].

	Vitamin E[b]					Selenium[c]				
	Day 90 Gest.		Parturition			Day 90 Gest.		Parturition		
Item	+E	-E	+E	-E	SE	+Se	-Se	+Se	-Se	SE
Lymphocyte Blastogenesis										
PHA[b]	4.90	4.54[e]	5.13	3.93[e]	.22	5.19	5.20	5.32	4.50	.21
PW[b]	5.19	4.64[e]	5.17	3.79[e]	.20	5.28	5.18	5.31	4.67	.23
Blood polymorphonuclear immune response										
Phagocytic, %	90.7	86.2[e]	90.1	83.8[e]	2.3	92.9	80.5*	90.2	72.2[e]	3.2
Microbicidal	57.6	48.7[e]	58.1	40.6[e]	2.6	53.1	38.4*	56.3	34.3[e]	2.9

[a]Source: Wuryastuti et al. (1993).

[b]Fortified diets contained vitamin E at 60 IU/kg.

[c]Fortified diets contained Se at .3 ppm.

[d]The immunoresponsiveness of the lymphocytes was assessed by measuring their responses to phytohemagglutin (PHA) and pokeweed (PW) mitogens.

[e]Significant response ($P < .05$).

Table 12. *Phagocytic and microbicidal activities of polymorphonuclear (PMN) cells of colostrum and milk from control sows and sows fed vitamin E- and(or) selenium-depleted diets between conception and 4 days postpartum*[a].

	Phagocytic activity[b]		Microbicidal activity[c]	
Diet	Colostrum	Milk	Colostrum	Milk
Neg. Control (No E/Se)[d]	35.2 ± .9[e]	21.2 ± 2.5	3.2 ± 2.7[e]	1.2 ± .1[e]
Control (+E/Se)[d]	50.2 ± 5.4	27.5 ± 3.0	6.2 ± .8	2.7 ± .2
(-E)	43.6 ± 3.2	23.7 ± 1.5	3.6 ± .6[e]	2.2 ± .5
Control (+E/Se)[d]	44.6 ± 8.3	30.2 ± 5.0	6.2 ± 1.0	2.4 ± .1
(-Se)	33.4 ± 5.1	19.9 ± 3.4	2.6 ± .6[e]	1.6 ± .4

[a]Source: Wuryastuti et al. (1993).
[b]Percentage of PMN cells containing two or more yeast particles.
[c]Percentage of PMN cells containing two or more dead yeast particles.
[d]Control diets were fortified with vitamin E (IU/kg) and Se (.3 ppm) while treatment diets deleted one or both nutrients.
[e]Significantly ($P < .05$) different from respective control.

Table 13. *Commercially available sources of vitamin E and their relative biological activities*[a]

Source	Identification	Activity (IU/mg)
Synthetic		
	all-rac-α-tocopherol (dl)	1.1
	all-rac-α-tocopheryl acetate[b]	1.0
Natural		
	RRR-α-tocopherol (d)	1.49
	RRR-α-tocopheryl acetate[b]	1.36

[a]Source: U.S. Pharmacopeia and National Formulary (1980).

[b]Esters are attached to improve stability of the product.

Table 14. *Recommended dietary selenium and vitamin E levels for swine*

Production Phase	Se (ppm)	Vitamin E (IU/ton)[a]
Nursery	.3	60,000
Grower	.2	40,000
Finisher	.1	20,000
Gestation	.3[b]	60,000
Lactation	.3[b]	60,000
Boars	.3[b]	60,000

[a]Recommendations are based on the use of dl α-tocopheryl acetate.

[b]When organic Se is approved, it is recommended that 100% be used as the supplemental Se source.

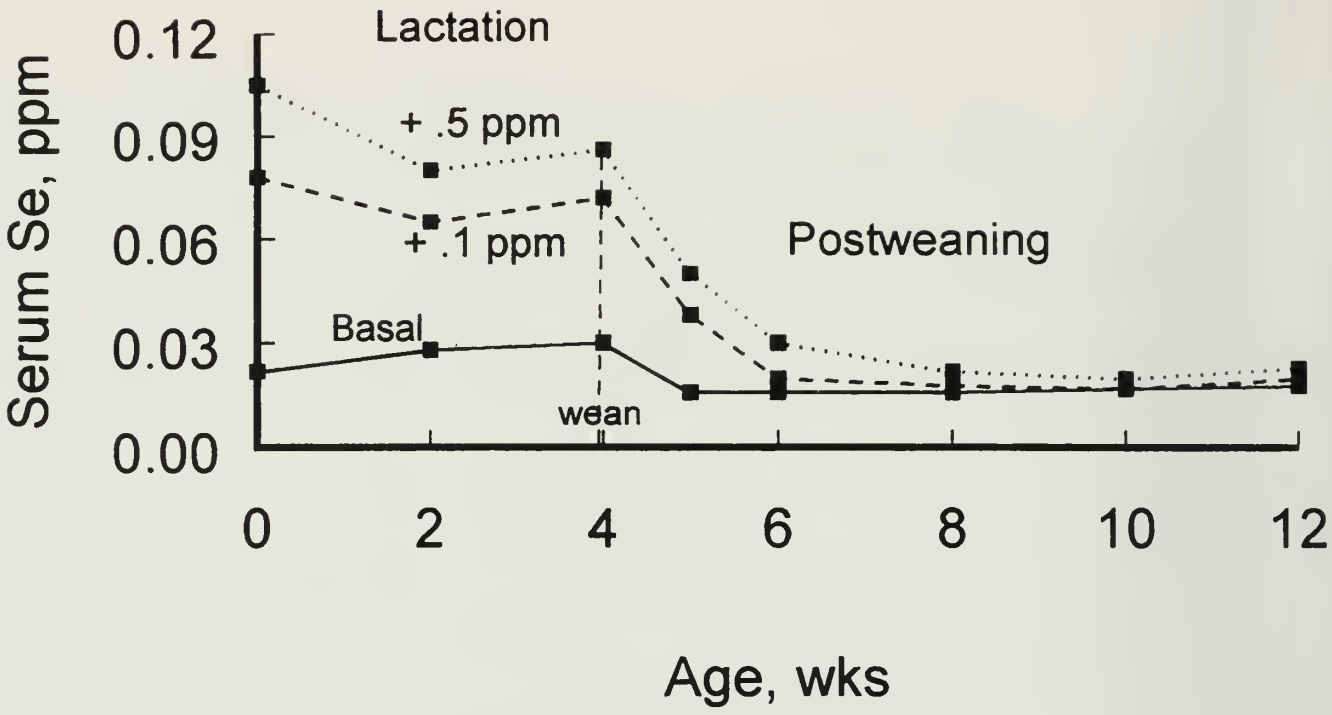

Figure 1. The effect of sow dietary selenium levels on progeny serum selenium concentrations (Mahan et al., 1977).

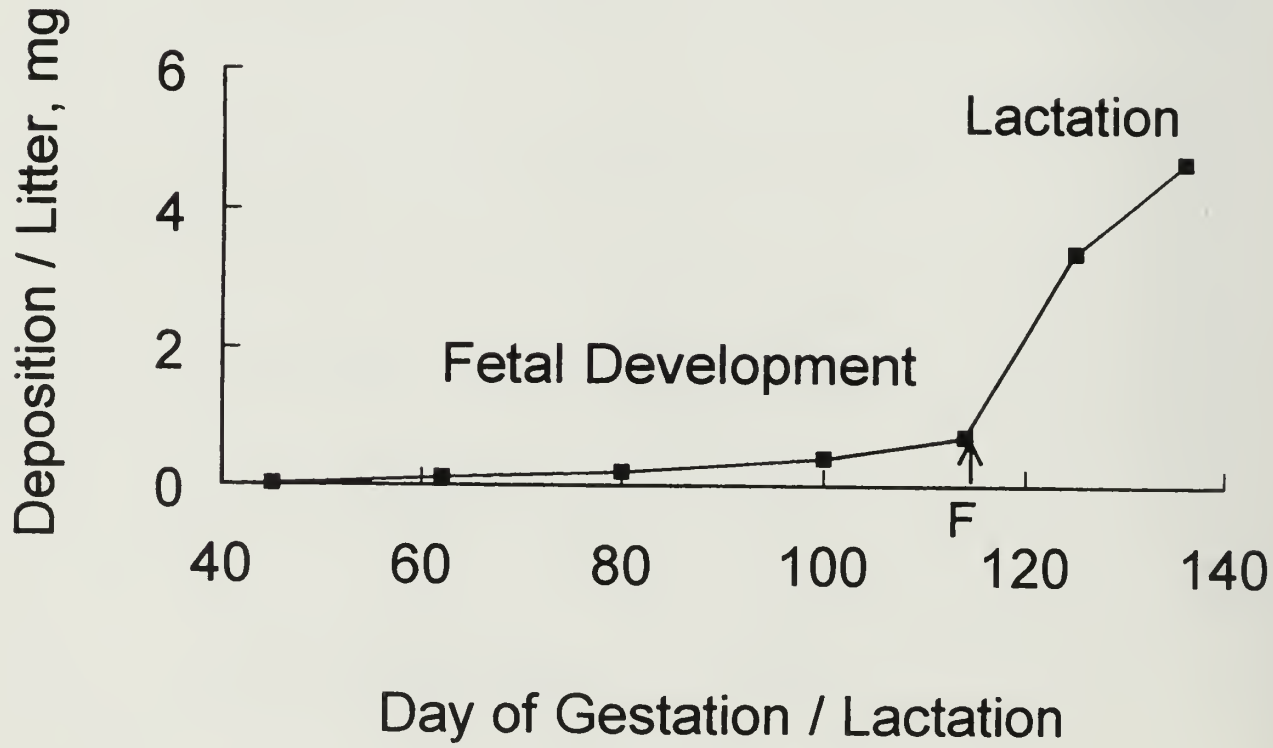

Figure 2. Litter accumulation of selenium during fetal development and lactation.

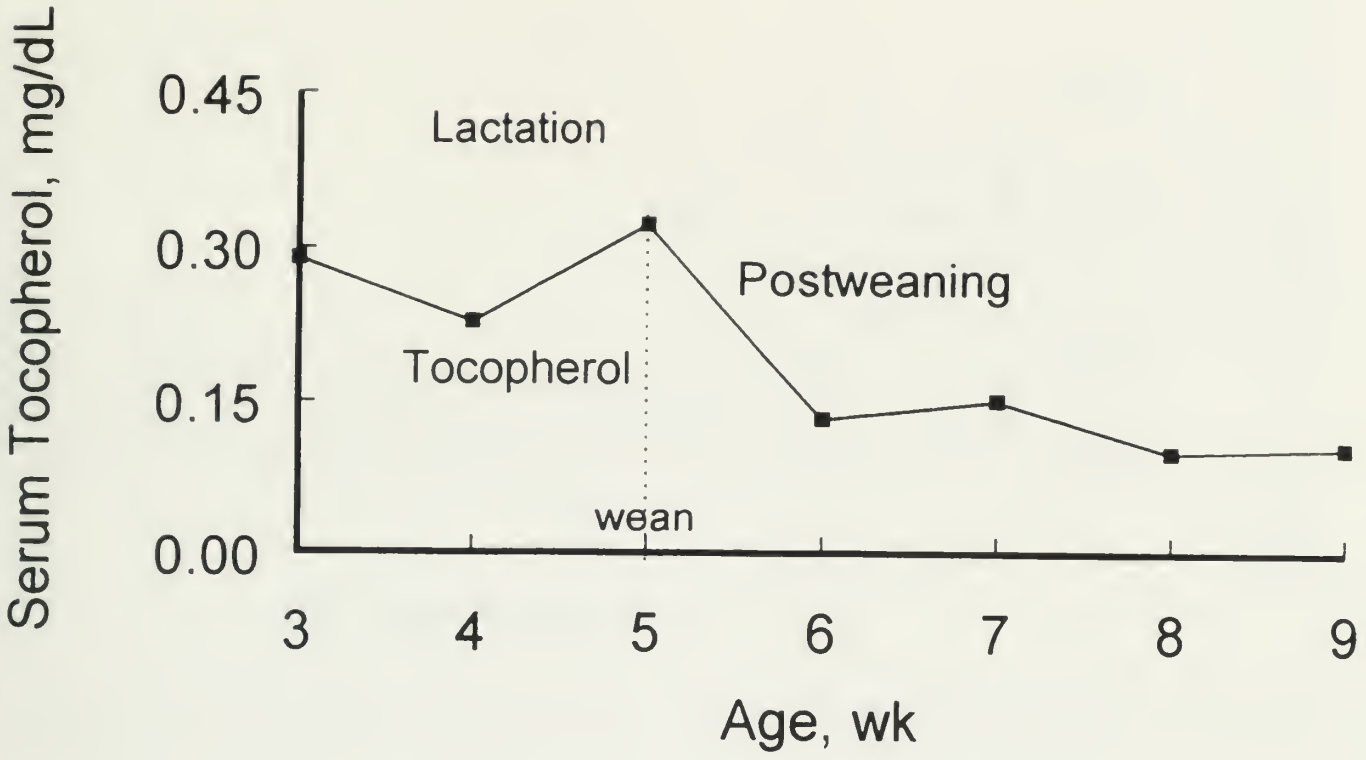

Figure 3. Serum tocopherol concentrations in pigs during lactation and the immediate weeks postweaning (Mahan and Moxon, 1980).

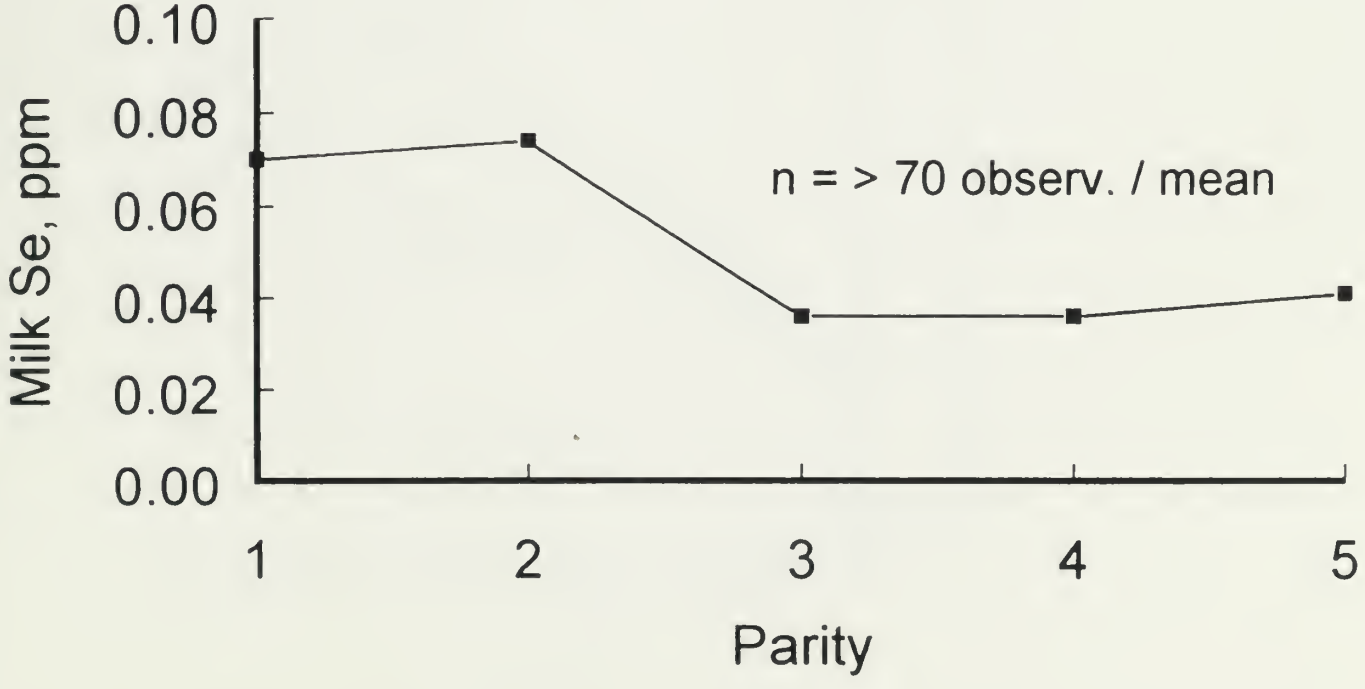

Figure 4. Milk (21-day) selenium concentrations in sows from parity 1 to 5 (Mahan, 1991; 1994).

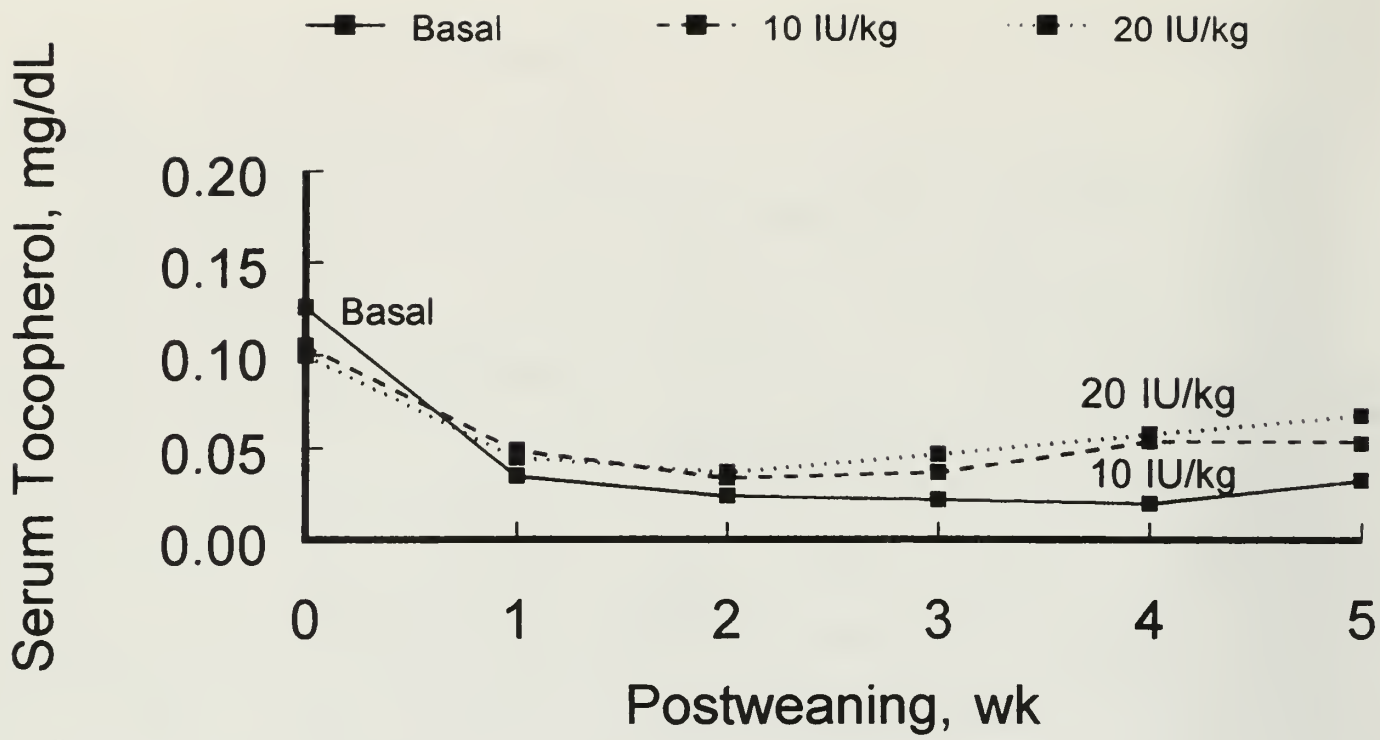

Figure 5. Effect of dietary vitamin E levels in weanling pigs on serum tocopherol (Meyer et al., 1981).

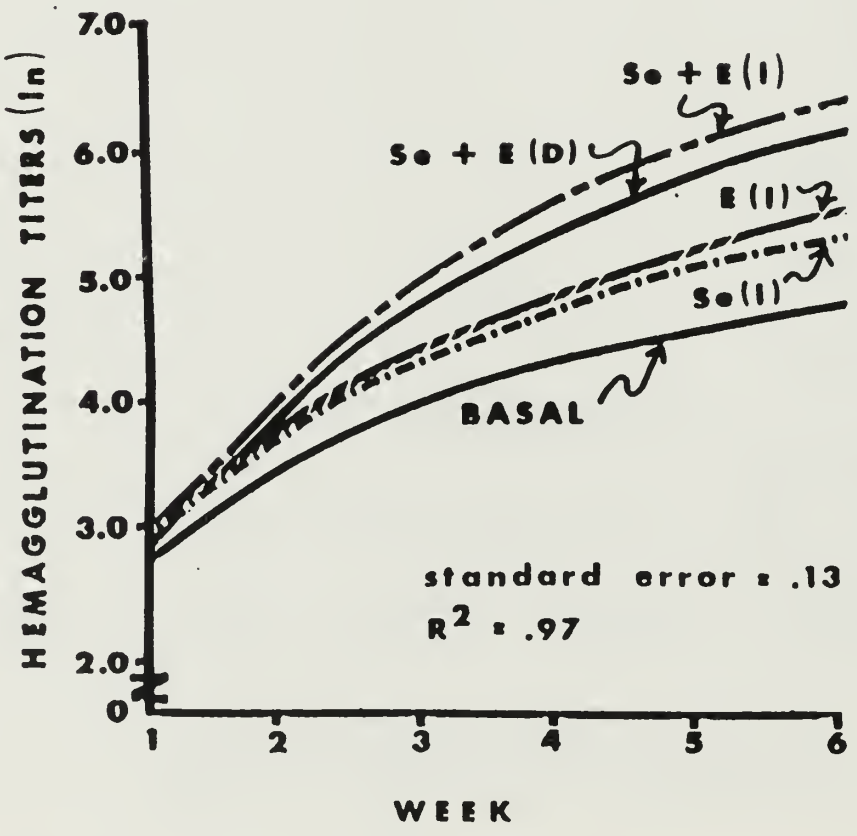

Figure 6. Effect of dietary or injected vitamin E and(or) selenium on postweaning pig antibody titers (Peplowski et al., 1980).

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